FLORA OF AUSTRALIA

Volume 1
Introduction
2nd edition

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FLORA OF AUSTRALIA

The *Flora of Australia* is intended to provide, for the first time in over 100 years, a uniform description of the plants of Australia, with keys to enable them to be identified, and with information on the distribution and ecology of each taxon. In addition it will illustrate most genera and many species, and where appropriate, provide review essays of various aspects of the Australian flora. The text is designed to be used by all who have an interest in the flora, with technical terms kept to a minimum, a glossary, and succinct descriptions.

This new edition of the original introductory volume contains entirely new essays on many aspects of the flora, and Australian plant taxonomy. Included are essays on the history and bibliography of plant taxonomy, evolution or the climate and land forms, palaeobotany, the present climate and vegetation types, biogeography, utilisation and conservation of the Australian flora.

The *Flora of Australia* is a tool to be used by biodiversity managers, field naturalists, students, biologists and community groups, and an encyclopaedic work for botanists and plant enthusiasts.

Cover: Australia’s national floral emblem, *Acacia pycnantha* Benth., painted by Bryony Fremlin.

Contents of volumes in the *Flora of Australia*, the families (current at December 1998) arranged according to the system of A.Cronquist (1981).

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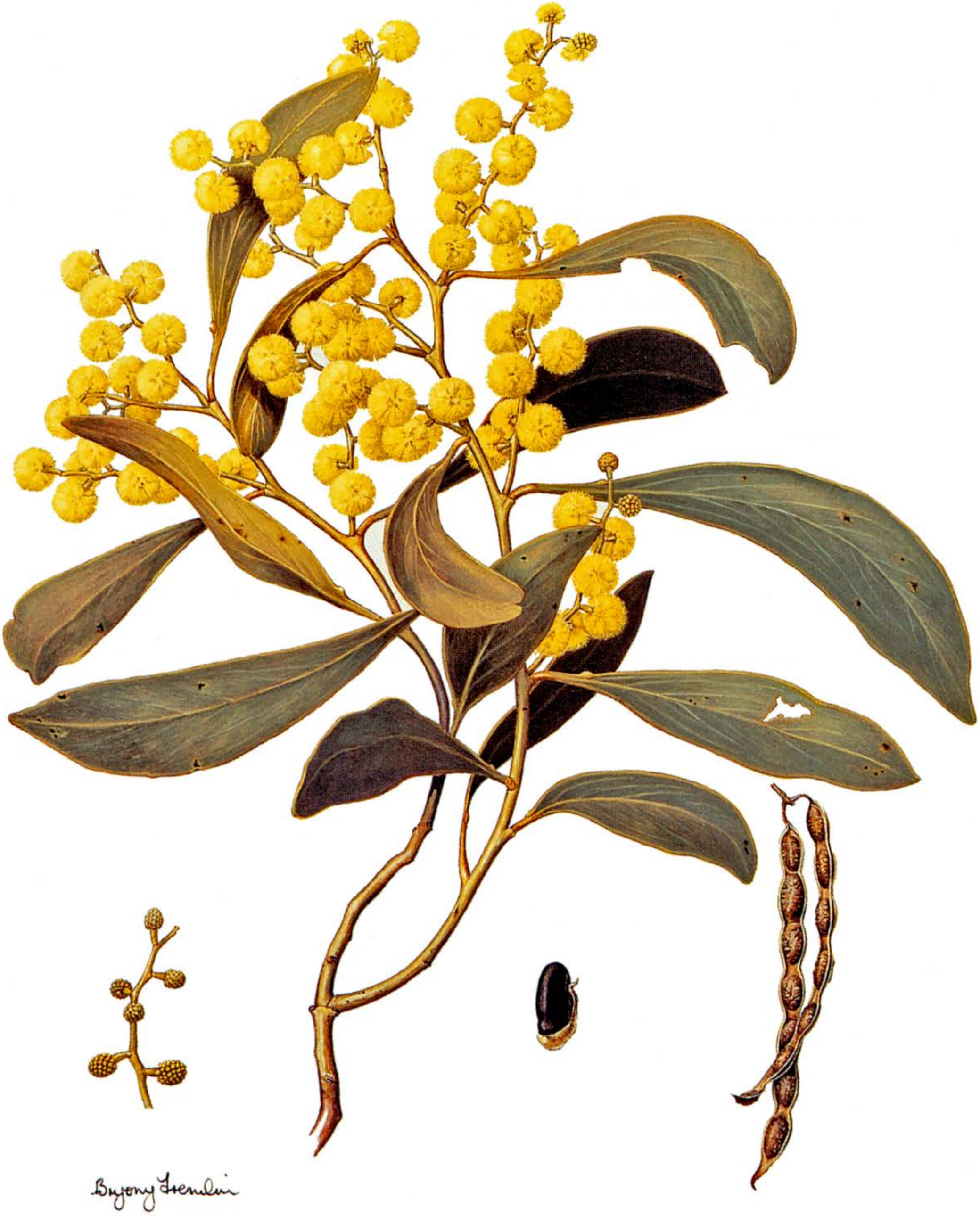

Australia’s national floral emblem, *Acacia pycnantha* Benth. Painting by Bryony Fremlin.

A publication of the
AUSTRALIAN BIOLOGICAL RESOURCES STUDY, CANBERRA

FLORA OF AUSTRALIA

Volume 1
Introduction
2nd edn

Environment Australia
Department of the Environment and Heritage

CSIRO

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This work may be cited as:

Flora of Australia Volume 1, Introduction, 2nd edn. Melbourne : ABRS/CSIRO Australia (1999).

Individual contributions may be cited as:

L.Frakes, Evolution of Australian Environments, *Flora of Australia*, 2nd edn, 1: 163–203 (1999).

First published 1981
Second edition 1999

This book is available from:

CSIRO PUBLISHING
PO Box 1139 (150 Oxford Street)
Collingwood VIC 3066
Australia

Tel: (03) 9662 7666 Int: +(61 3) 9662 7666
Fax: (03) 9662 7555 Int: +(61 3) 9662 7555

Email: sales@publish.csiro.au

National Library of Australia
Cataloguing-in-Publication entry

Flora of Australia. Volume 1, Introduction, 2nd edn.

Bibliography.
Includes index.
ISBN 0 643 05965 2 (hard cover).
ISBN 0 643 05702 1(hard cover set).
ISBN 0 643 05695 5(soft cover set).
1. Botany – Australia – Classification. 2. Plants – Identification. I. Australian Biological Resources Study. II. CSIRO.
581.994

Published by ABRS, Canberra/CSIRO, Melbourne
Printed in Australia by Brown Prior Anderson

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ACKNOWLEDGMENTS

There are 20 contributors, six illustrators and 18 photographers to Volume 1. Their co-operation is gratefully acknowledged.

The Australian National Botanic Gardens slide collection provided a number of the colour photographs used in this volume, and we wish to express our appreciation to Jan Wilson and Murray Fagg for their continued help and generosity. These slides are individually identified by the initials ANBG in the relevant figure captions.

Catherine Jordan and Linda Harris, the Librarians at the Australian National Botanic Gardens, were as always cheerful and extremely helpful in assisting to locate references.

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The assistance of Maria Cofinas, Gaston Rozenbilds, Gavan Thomas, Dougal Torrance, Greg Whitbread and Mellissa Wood in preparation and supply of some of the maps is greatly appreciated.

John Huisman coordinated commissioning of the Aquatic Botany chapter and wrote the link passages.

The co-operation of many referees, usually working to tight deadlines, is also acknowledged.

The production of this volume would not have been possible without the substantial assistance of the Australian State and University Herbaria. Their willingness to provide staff time and resources for this project of national importance is an outstanding example of co-operation between the States and the Commonwealth.

The Executive Editor acknowledges with great pleasure the editing input by staff of the Australian Biological Resources Study. Their work, invisible in the final product, is onerous, often tedious, but essential in maintaining the high standards that this series has achieved. Checking and bromiding of illustrations was undertaken by Jane Mowatt. Most ABRS Flora Section staff were involved at various stages in writing, editing, indexing and collating the text.

The co-operation of CSIRO Publishing in bringing this book to press is gratefully acknowledged.

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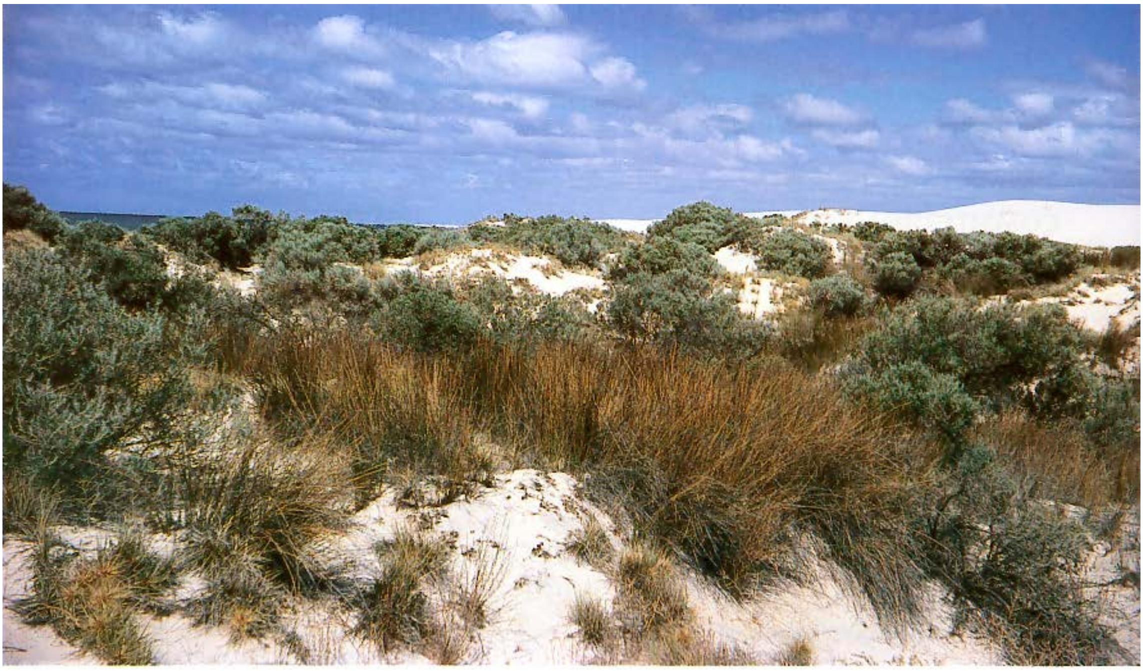

Figure 1. Saltbush (*Atriplex*) and sedges on coastal sand-dunes near Cowell, S.A.
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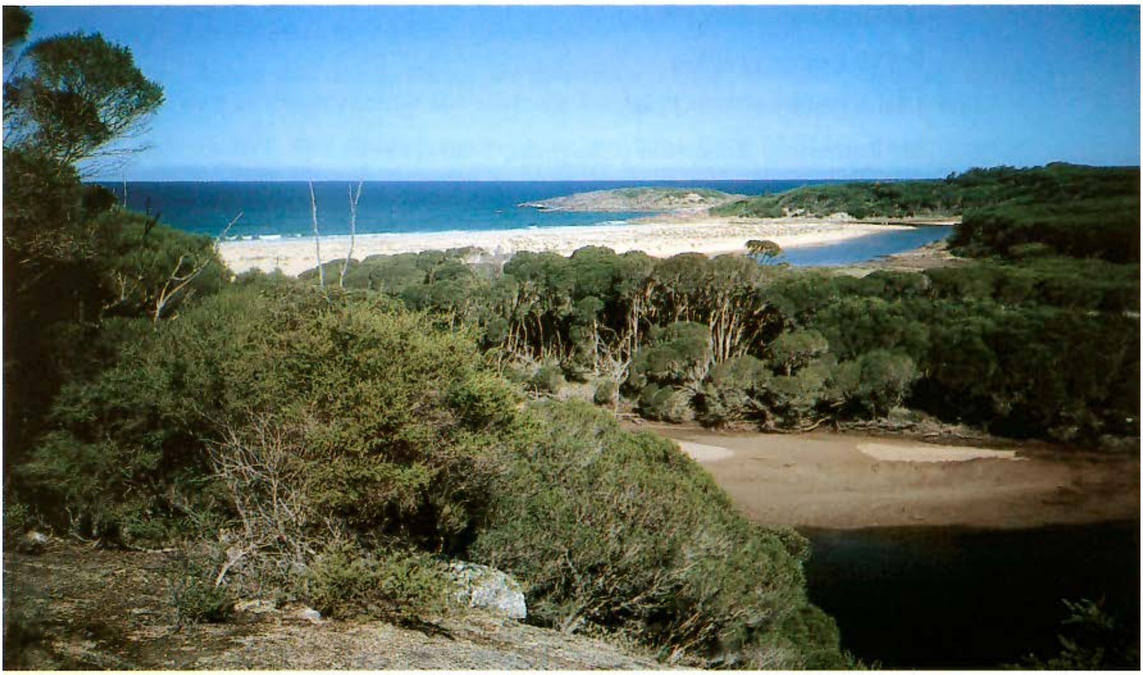

Figure 2. *Melaleuca* thicket, margins of coastal wetland, between Tathra and Bermagui, N.S.W.
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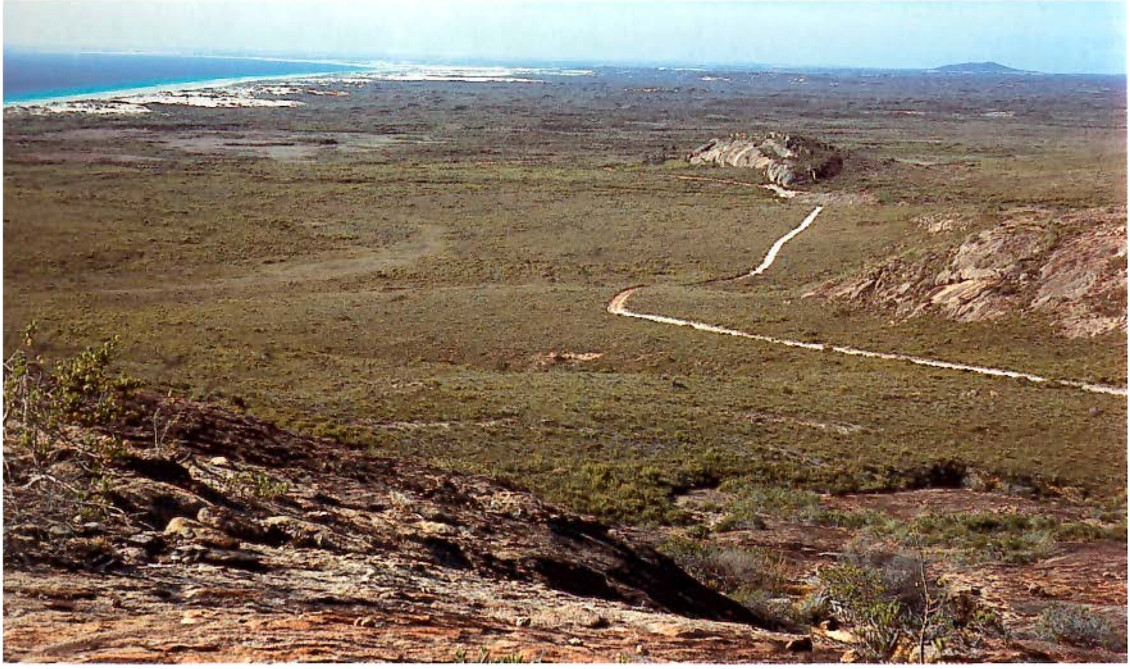

Figure 3. Coastal scrub heath (kwongan), Cape Le Grande National Park, W.A.
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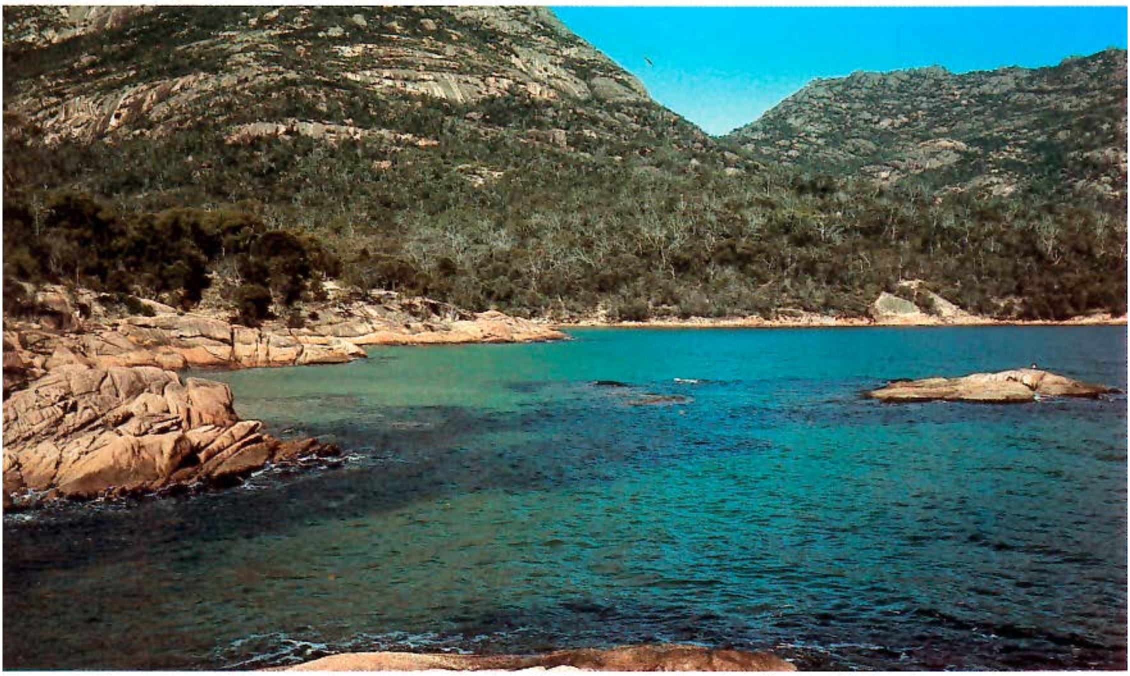

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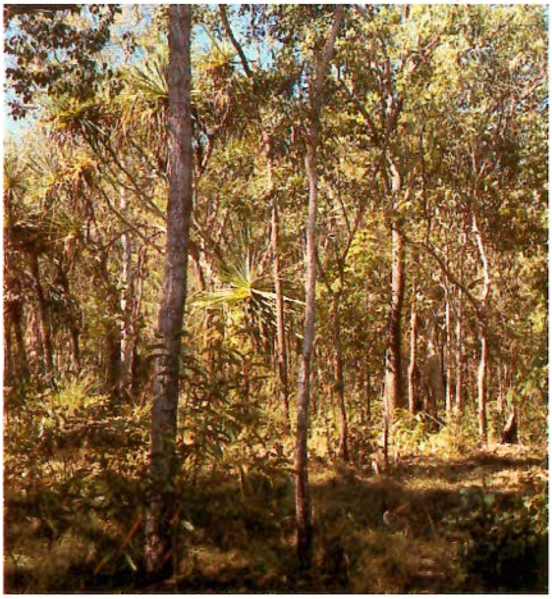

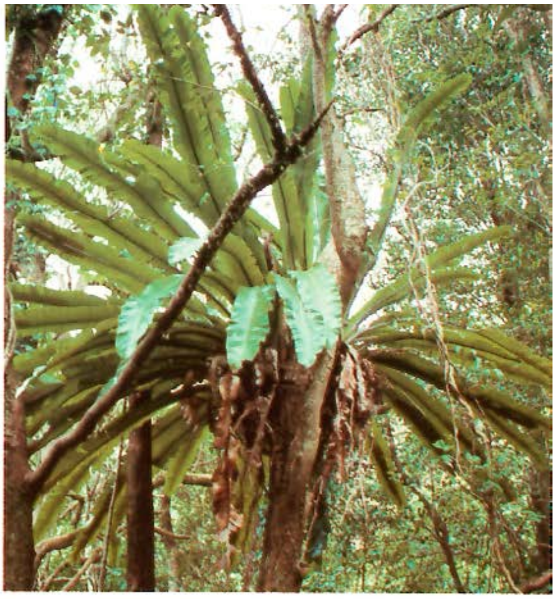

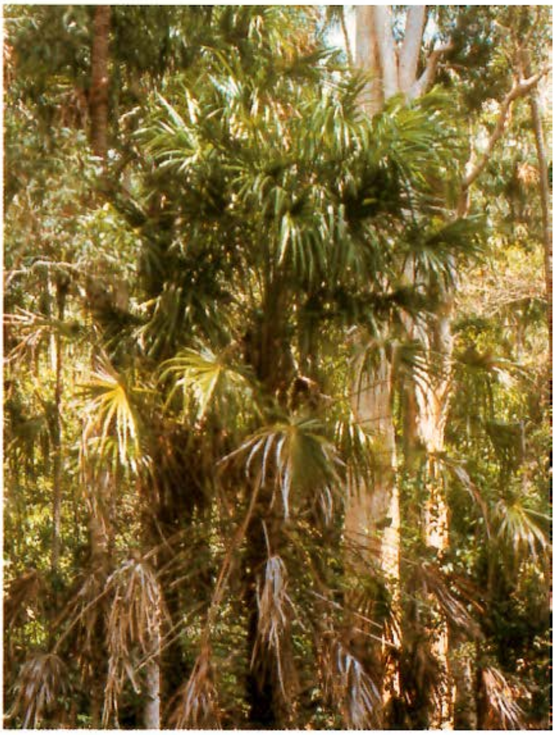

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Photograph — A.E.Orchard.

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Photograph — A.Wells.

Figure 7. Perching epiphyte (*Asplenium australasicum*) & lianes, closed forest, Minnamurra Falls, N.S.W. Photograph — R.Hotchkiss (ANBG).

Figure 8. Monsoon forest, with *Melaleuca quinquenervia* and *Livistona benthamii*, Lockhart River, Qld. Photograph — J.W.Wrigley (ANBG).

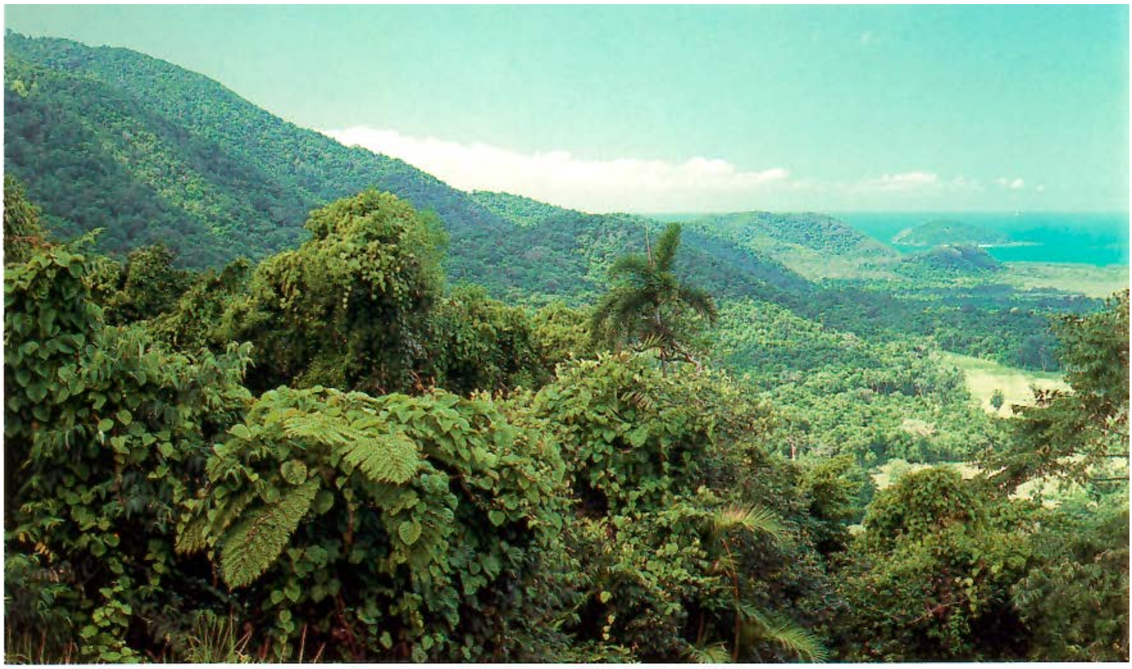

Figure 9. Complex mesophyll vineforest, near Cape Tribulation, Qld.
Photograph — V.J.Nelder.

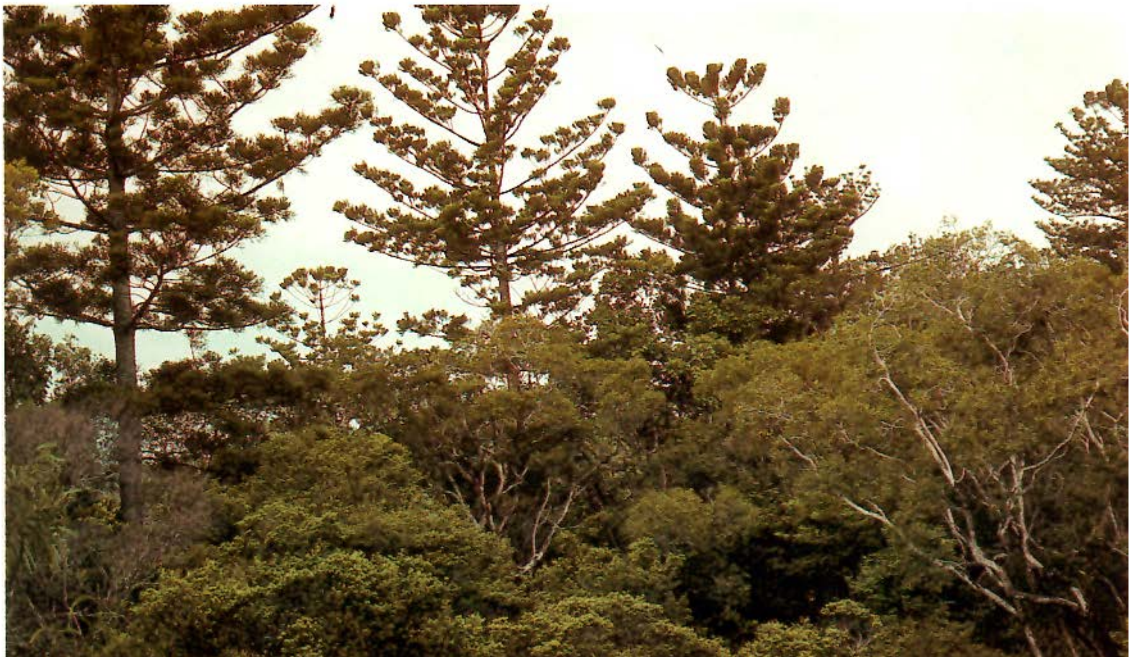

Figure 10. *Araucaria cunninghamii* emergents above evergreen notophyll vine forest, SSW of Cape Flattery, Cape York Peninsula, Qld.
Photograph — V.J.Nelder.

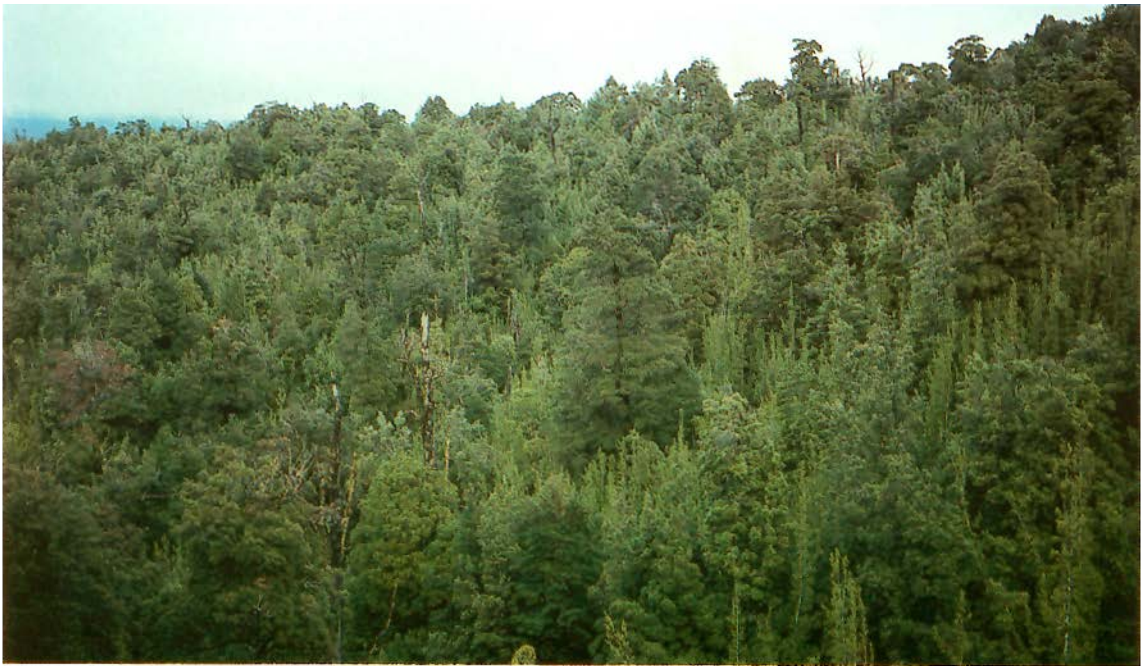

Figure 11. Cool temperate rainforest with *Nothofagus cunninghamii*, *Eucryphia lucida* and *Anodopetalum biglandulosum*, Savage River, Tas. Photograph — G.Kantvilas.

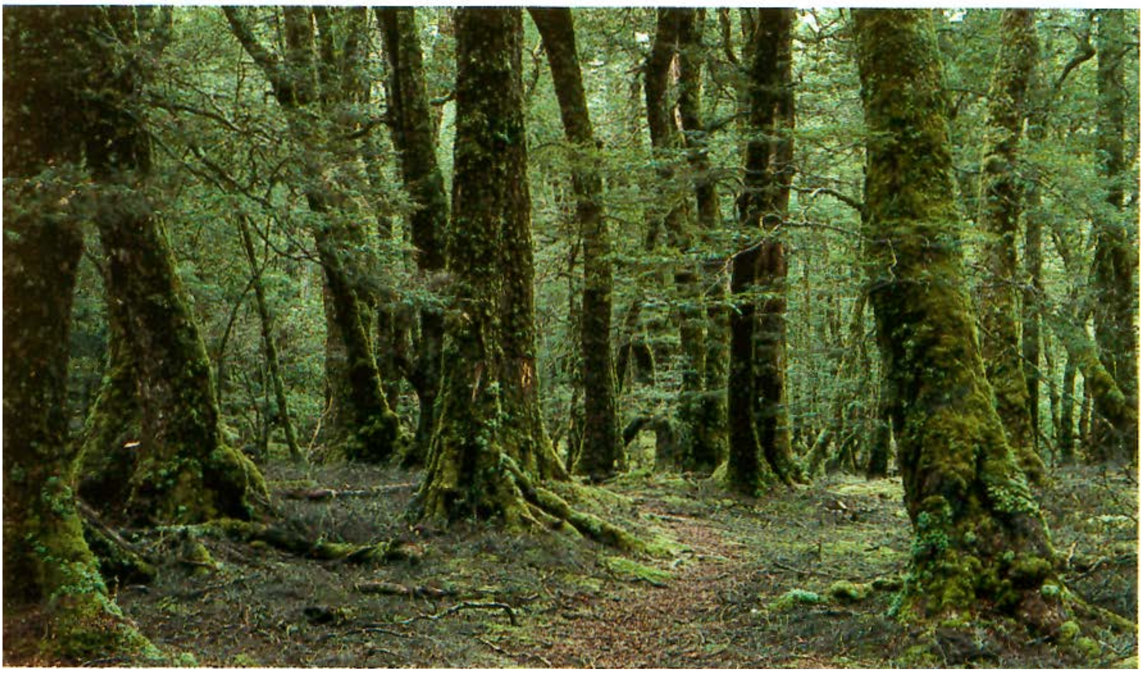

Figure 12. Cool temperate rainforest (high altitude callidendrous) dominated by *Nothofagus cunninghamii*, Little Fisher River, Tas.
Photograph — S.J.Jarman.

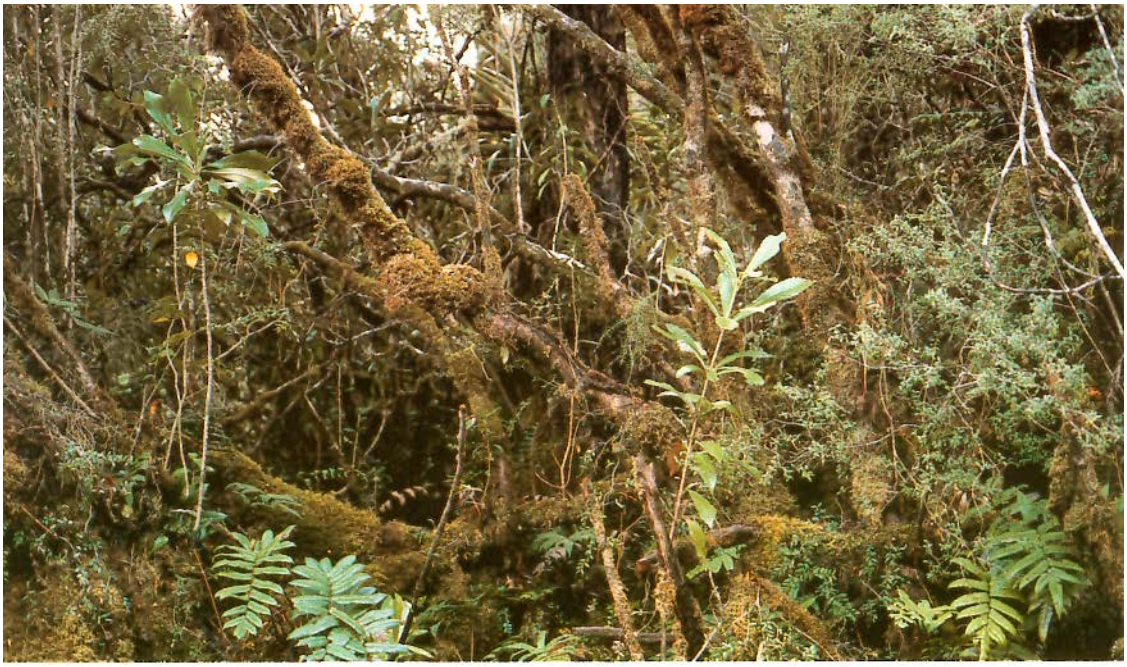

Figure 13. Cool temperate rainforest (implicate) with tangle of *Anopterus glandulosus*, *Agastachys odorata*, *Eucryphia milliganii* and *Archeria eriocarpa*, Quinn Creek, western Tas. Photograph — S.J.Jarman.

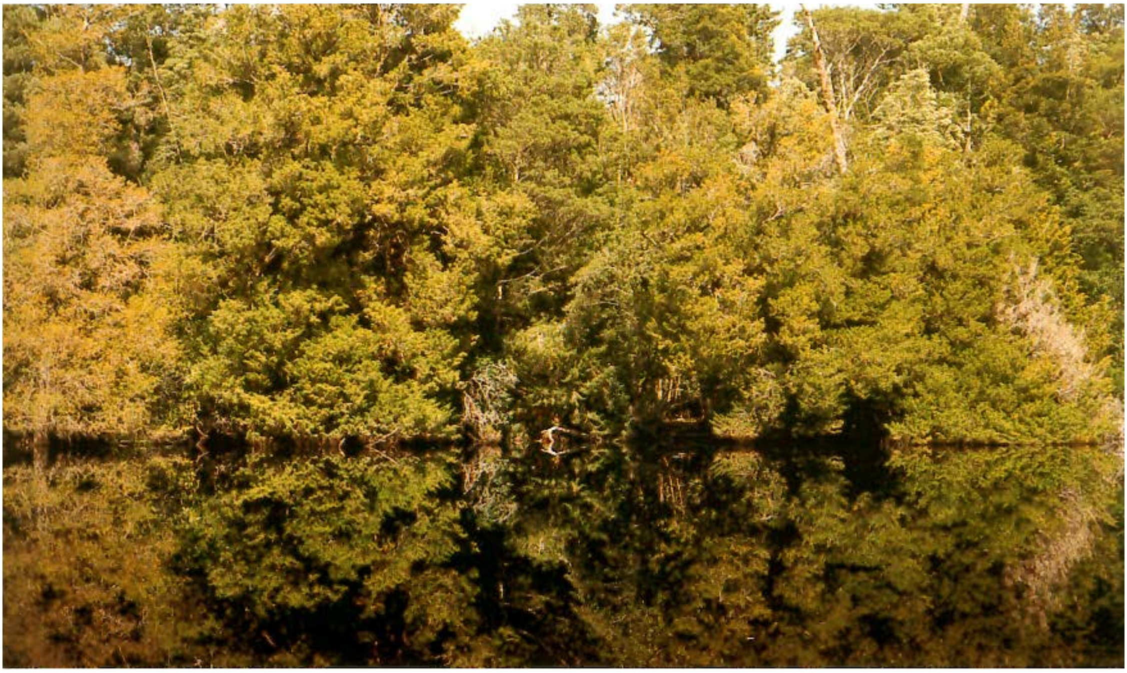

Figure 14. Riverine rainforest dominated by *Lagarostrobos franklinii*, Gordon River, Tas. Photograph — S.J.Jarman.

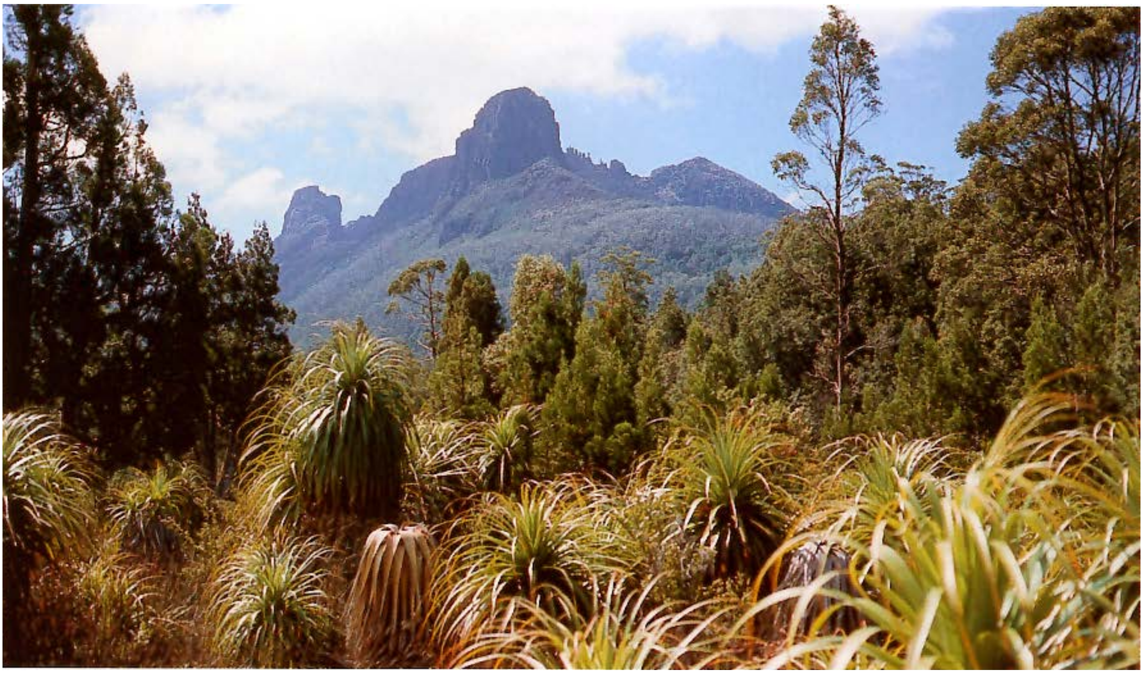

Figure 15. *Richea pandanifolia* at edge of cool temperate rainforest, Pine Valley, Tas.
Photograph — G.Kantvilas.

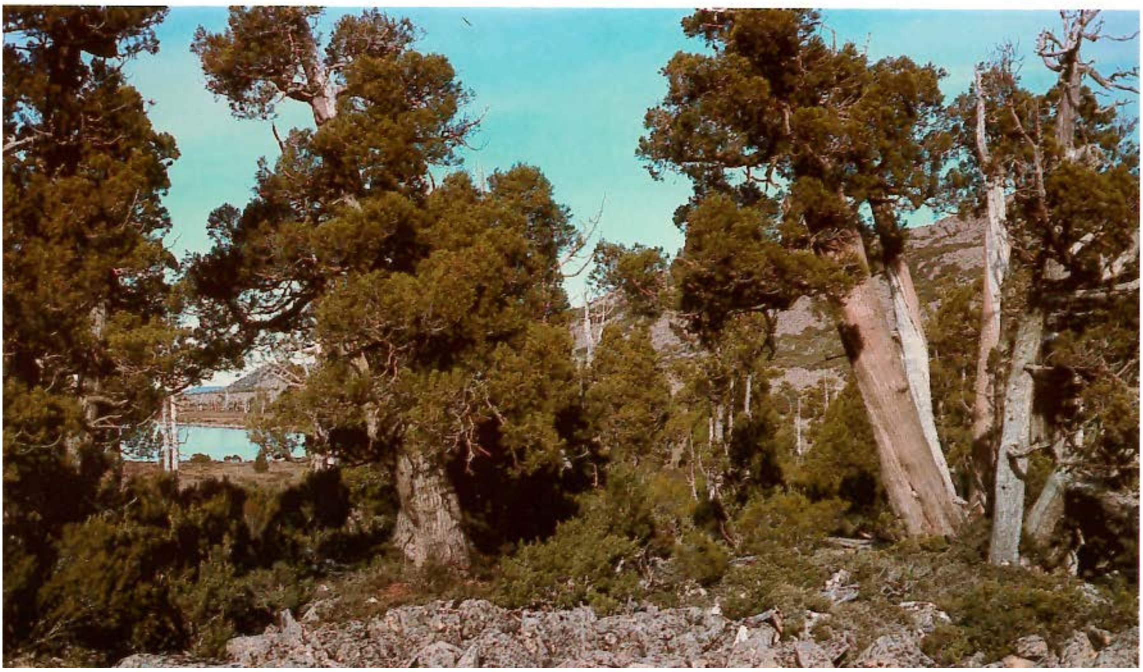

Figure 16. Open montane rainforest of *Athrotaxis cupressoides*, Pine Lake, Tas.
Photograph — G.Kantvilas.

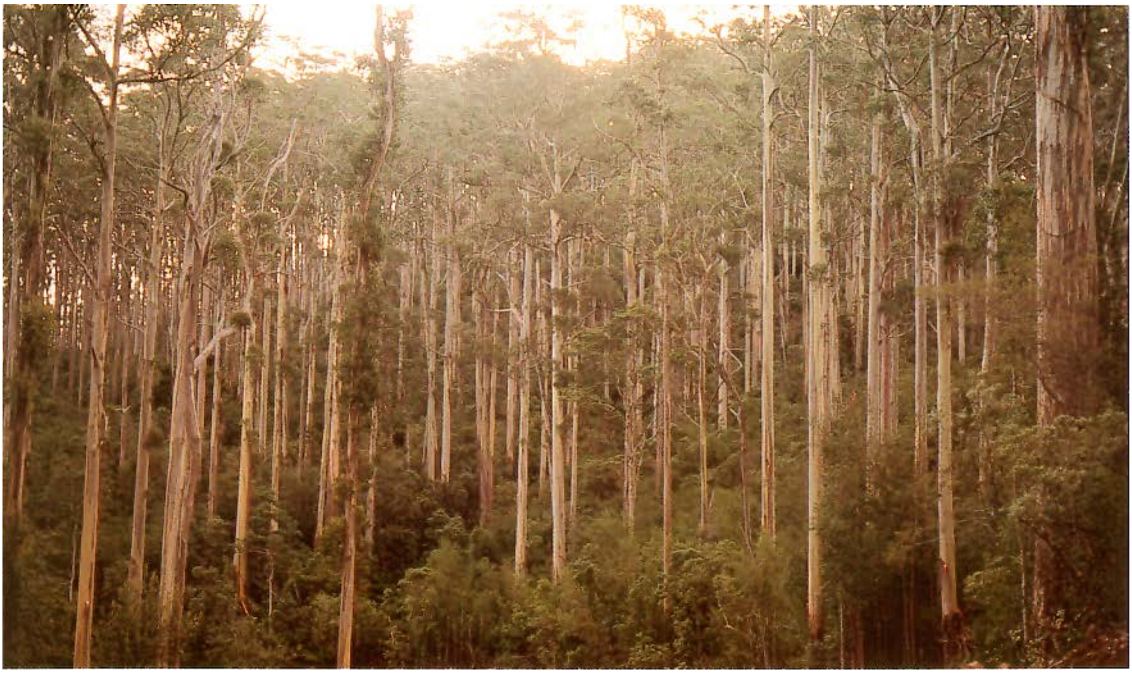

Figure 17. Wet sclerophyll forest (open-forest) with *Eucalyptus globulus* over *Bedfordia salicina*, Blue Gum Spur, Tas. Photograph — G.Kantvilas.

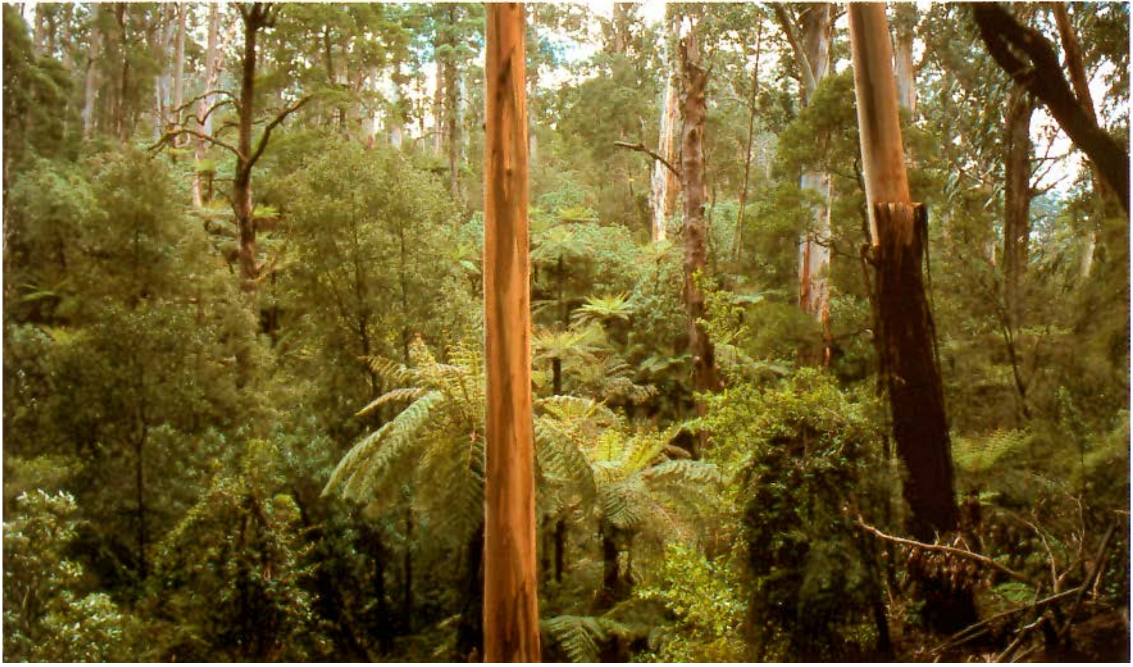

Figure 18. Wet sclerophyll forest (open-forest) Kallista–Belgrave Road, Dandenong Ranges, Vic. Photograph — M.Fagg.

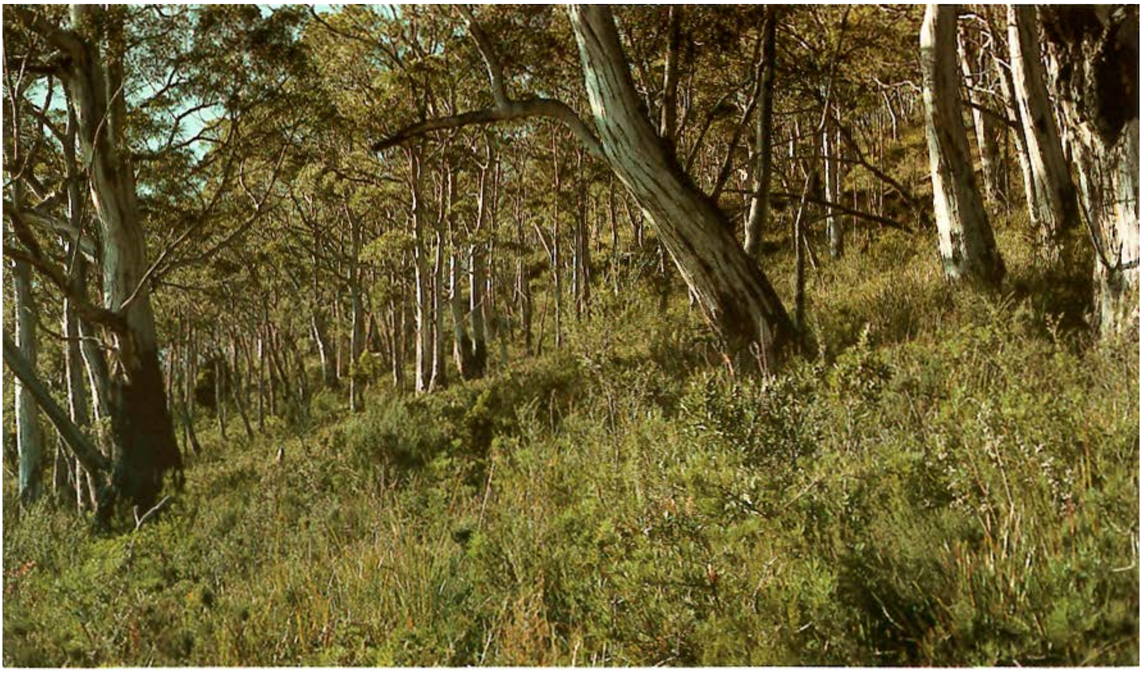

Figure 19. Dry sclerophyll forest (open-forest) with *Eucalyptus pulchella* over Epacridaceae, Fabaceae and Myrtaceae shrubs, Chimney Pot Hill, Tas. Photograph — G.Kantvilas.

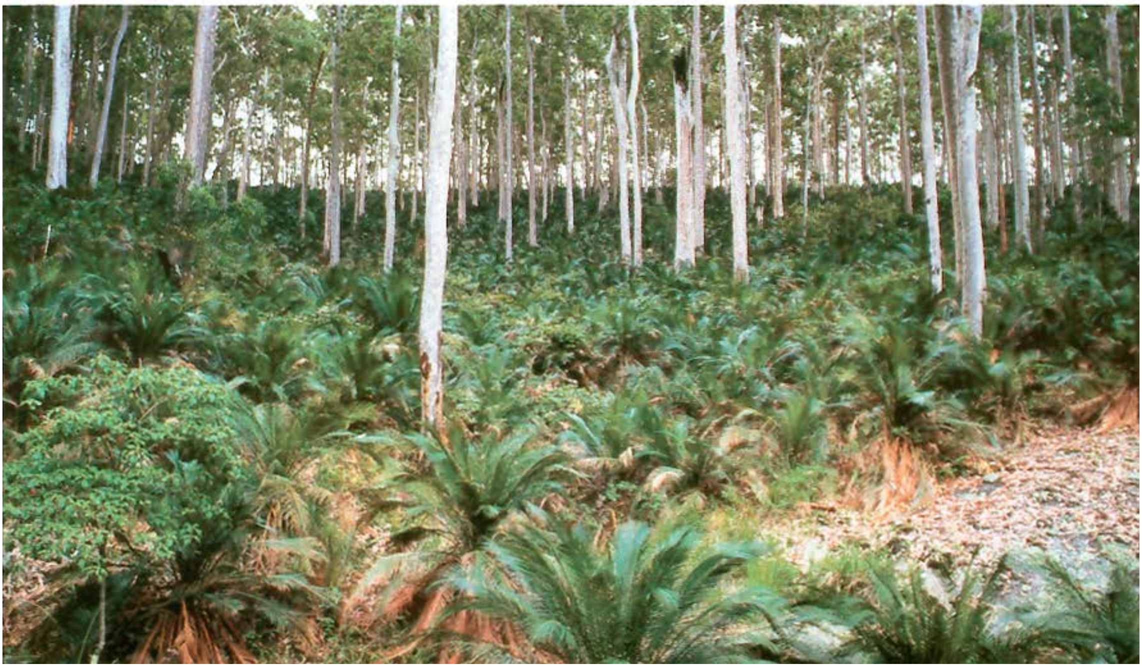

Figure 20. Dry sclerophyll forest (open-forest) with *Eucalyptus maculata* over *Macrozamia communis*, near Batemans Bay, N.S.W.
Photograph — M.Fagg.

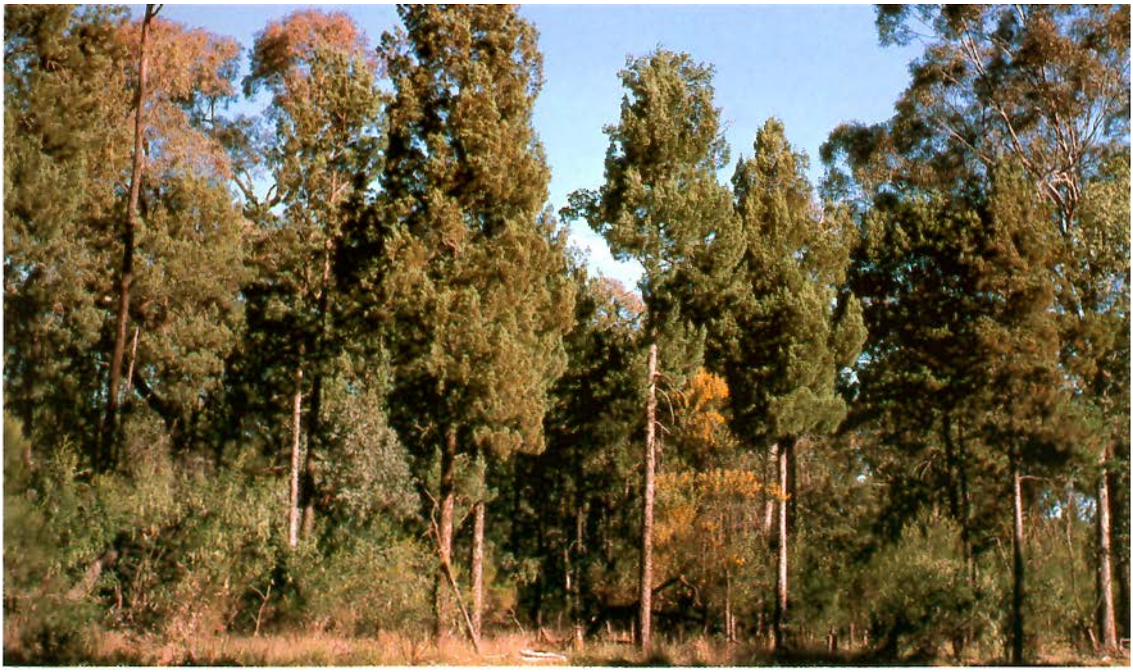

Figure 21. Woodland of *Callitris glaucophylla* and *Eucalyptus crebra*, Cumbil Road, Pilliga Scrub, N.S.W. Photograph — D.Greig (ANBG).

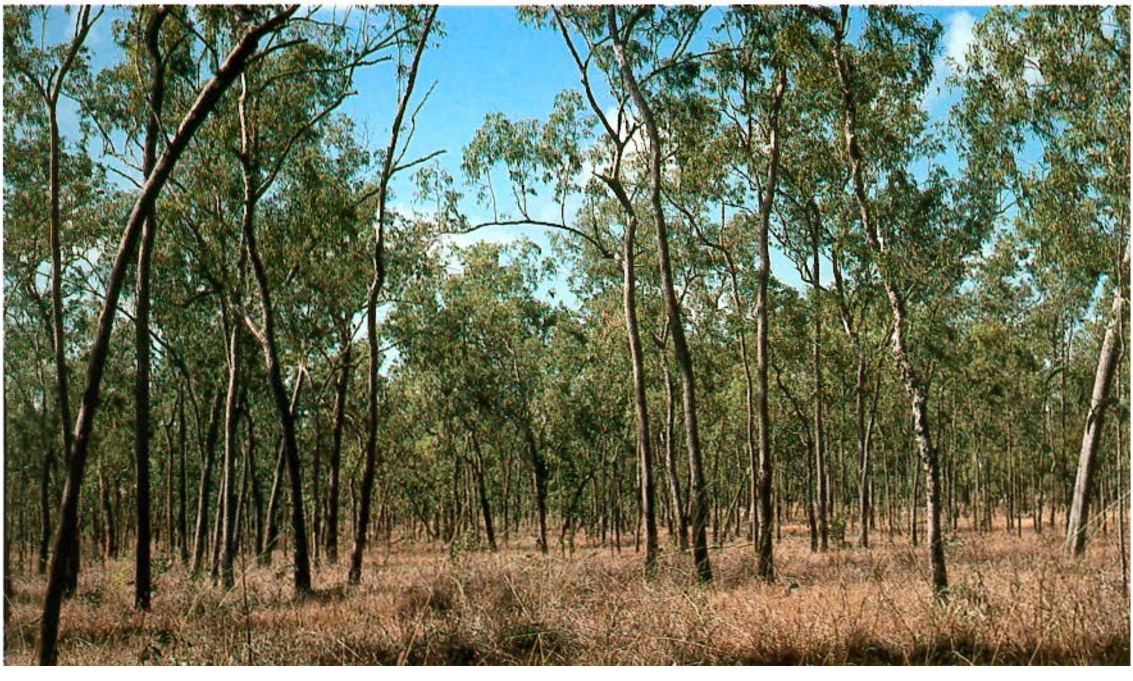

Figure 22. *Eucalyptus tetradonta* woodland, Cape York Peninsula, Qld. Photograph — J.R.Clarkson.

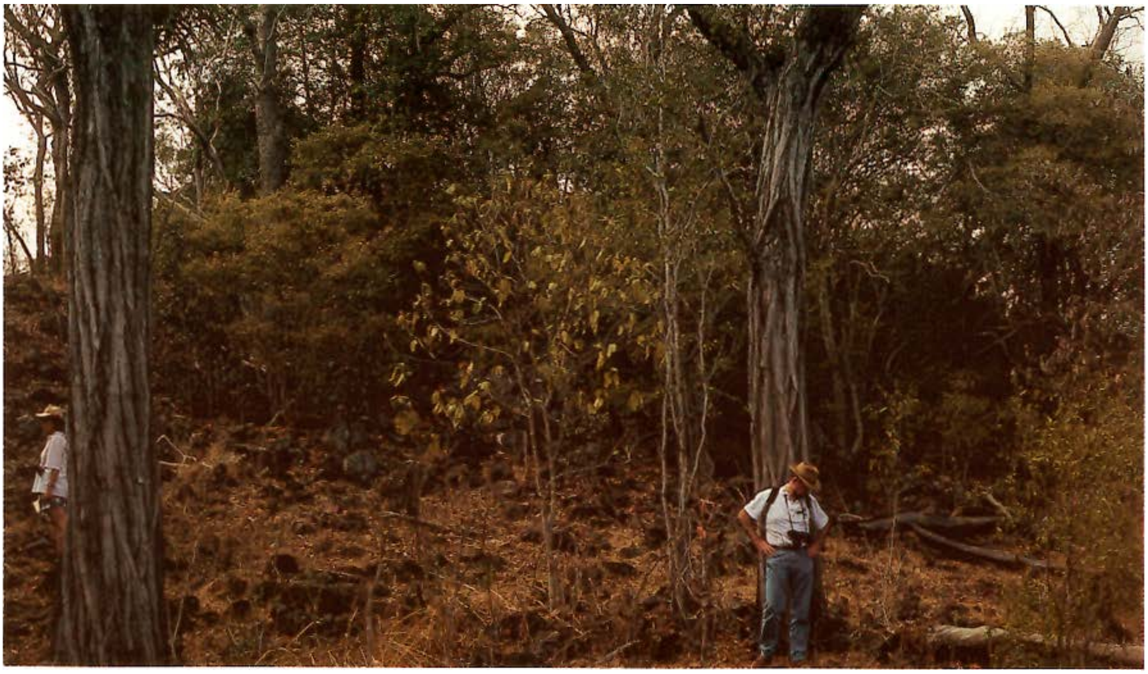

Figure 23. Deciduous vine thicket, with *Bombax ceiba*, *Canarium* sp. and *Brachychiton albidus*, near Bonney Glen, Qld. Photograph — M.D.Crisp.

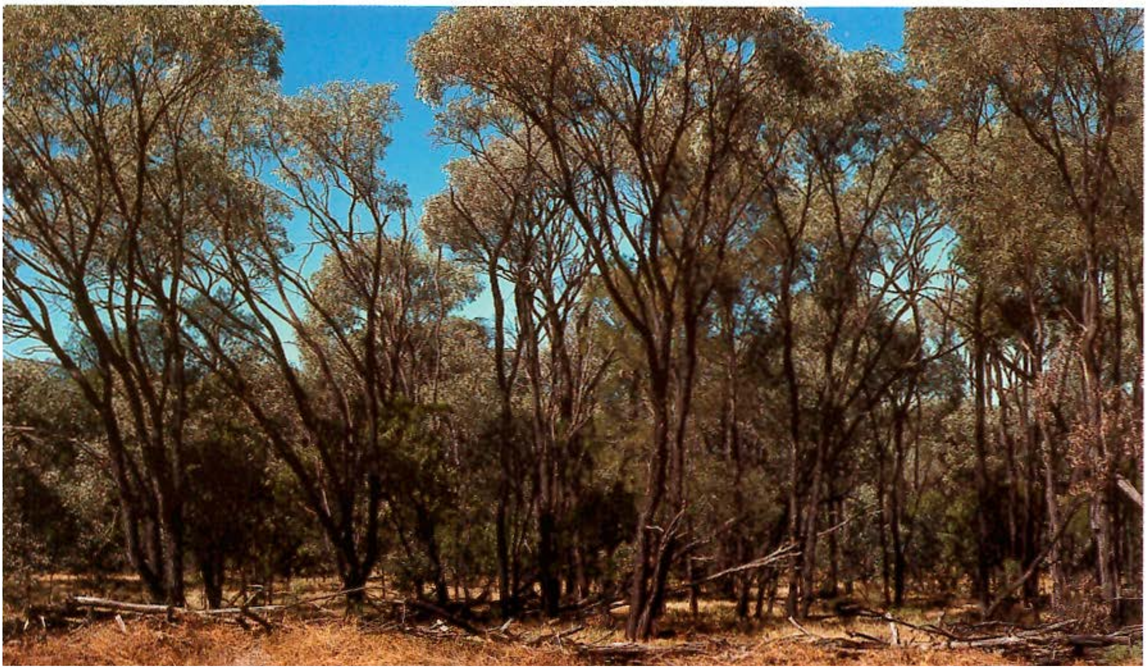

Figure 24. Brigalow (*Acacia harpophylla*) woodland with *Casuarina cristata*, north of Mitchell, Qld. Photograph — V.J.Nelder.

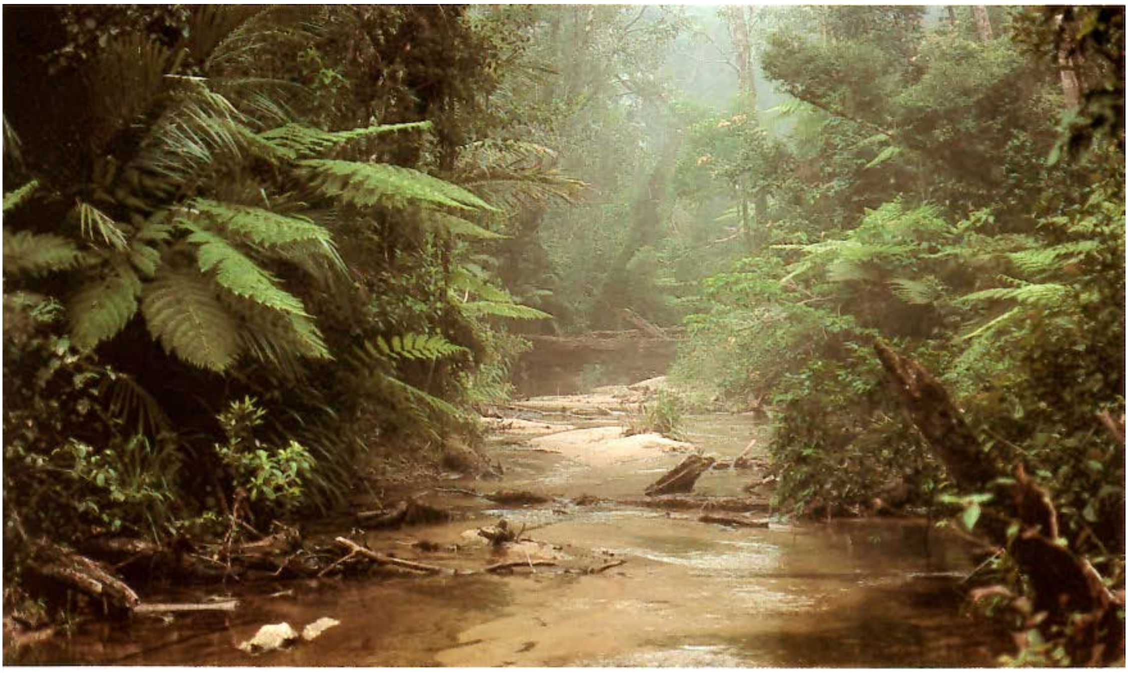

Figure 25. Complex mesophyll vineforest, Mount Lewis, Qld.
Photograph — J.R.Clarkson.

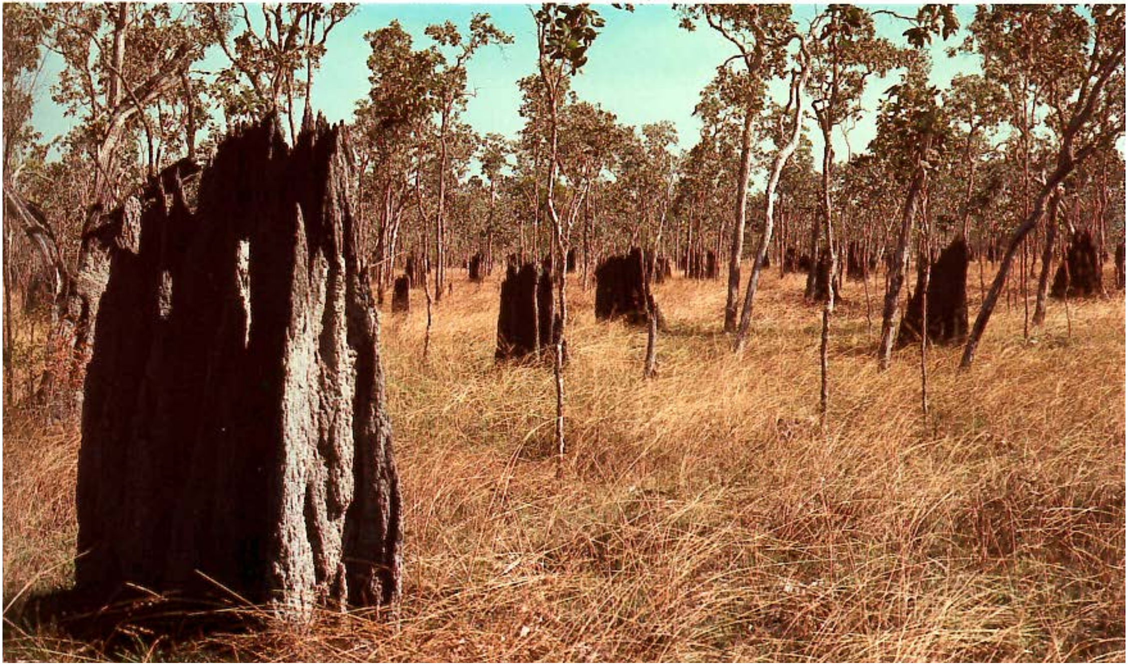

Figure 26. Low open woodland of *Melaleuca viridiflora*, near Sefton, Cape York Peninsula, Qld.
Photograph — J.R.Clarkson.

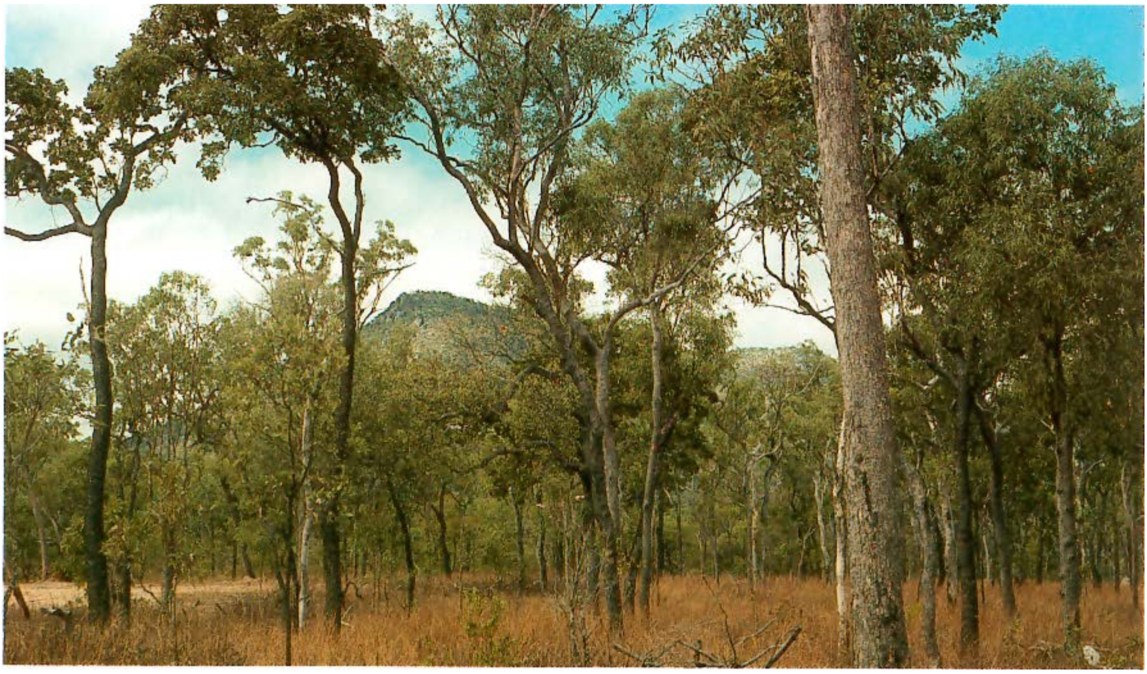

Figure 27. Open woodland of *Eucalyptus clarksoniana*, *E. cullenii*, *Erythroxylon ellipticum*, *Grevillea glauca* and *Heteropogon contortus*, Whites Creek near Mt Molloy, Qld.
Photograph — M.D.Crisp.

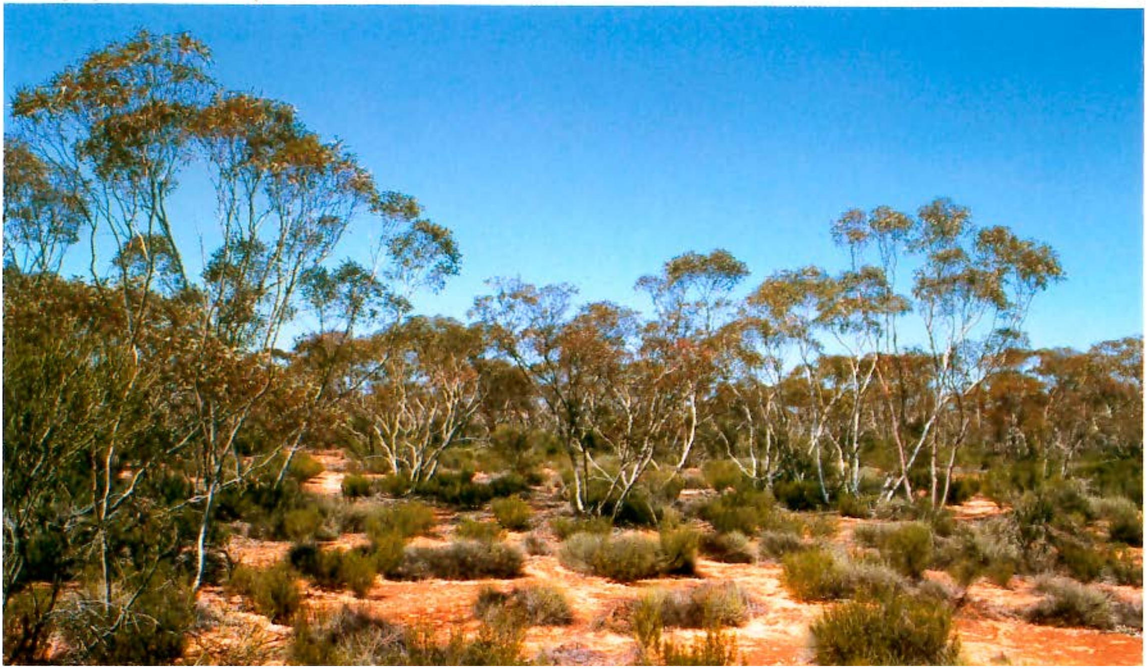

Figure 28. Mallee woodland of *Eucalyptus gracilis*, understorey of *Beyeria opaca* and *Triodia* hummocks, Calperum, near Renmark, S.A.
Photograph — M.Fagg (ANBG).

INTRODUCTION[1]

The *Flora of Australia* is intended to provide, for the first time in over 100 years, a uniform account of the plants of Australia, with keys to enable them to be identified, and with information on the distribution and ecology of each taxon. In addition it will have illustrations of most genera and a wide range of species, and in appropriate places, review essays of various aspects of the Australian flora. The text is designed to be used by all who have an interest in the flora, with technical terms kept to a minimum, a full glossary, and descriptions which are, within the limits of space available, comparable with each other. The *Flora of Australia* is a tool to be used by land managers, field naturalists, biologists and community groups, and an encyclopaedic work for students.

Despite 200 years of study and exploration, Australia's flora is still far from being completely catalogued, much less fully documented and understood. This was perhaps most starkly demonstrated by the discovery of a new monotypic genus of native pine, *Wollemia*, in 1994. The trees, to 40 m tall, were found in a gorge of Wollemi National Park, only 150 km from metropolitan Sydney. While this was one of the more spectacular discoveries of recent times, new native Australian species and genera in substantial numbers are routinely discovered in almost every revisional study undertaken. Only a limited number of censuses of the Australian vascular flora have been undertaken, but these show an accelerating rather than stabilising number of taxa in the Australian flora (Table 1).

Working documents developed by ABRS suggest that the increase in number of species known for Australia is continuing. Extrapolation to the completion of the first edition of the *Flora of Australia* suggests a total at that time of just over 20 000 species.

Table 1. Australia-wide censuses of Australian vascular plant species.

Reference	Number of taxa
J.E.Smith, *Specimen of the Botany of New Holland* (1793–1795)	27
J.E.Smith, *Exotic Botany* (1804–1805)	37
J.J.H. de Labillardière, *Novae Hollandiae Plant. Spec.* (1804–1807)	265
J.C.Dryander, Catalogue (unpublished) (1805)	370
R.Brown, *Prodromus Florae Novae Hollandiae...* (1810)	2040
R.Brown, *Botanical Appendix to Flinders' Voyage* (1814)	4200
R.Brown, *Botanical Appendix to C.Sturt, Narrative of an Expedition into Central Australia* (1849)	c. 7000
J.D.Hooker, *Introductory Essay, Flora Tasmaniae* (1856)	c. 7000
G.Bentham, *Flora Australensis* (1863–1878)	8125
F.Mueller, *Systematic Census of Australian Plants* (1882)	8646
F.Mueller, *Second Systematic Census* (1889)	8839
R.J.Hnatiuk (ed.), *Census of Australian Vascular Plants* (1990)	17 590

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[1] Compiled by A.E.Orchard, Australian Biological Resources Study, GPO Box 636, Canberra Australian Capital Territory 2601.

Species are distributed unevenly across Australia. Species rich areas occur in south-western Western Australia, Cape York Peninsula, NE Queensland in the Atherton district, SE Queensland/NE New South Wales, and in Tasmania. Hnatiuk (1990) gave the following totals for the vascular plants of the Australia States and Territories (Table 2). For some areas, more recent figures are given in parentheses:

Table 2. Numbers of vascular plant species in each Australian State and Territory (N.S.W. includes A.C.T.), and these numbers expressed as a percentage of the total flora (from Hnatiuk, 1990).

State/Territory	Native species	Naturalised species	Total species described	% of total described flora	% of total land area[6]
Western Australia	7463	853	8316	47.3%	32.87%
Northern Territory	3293 (3604[1])	262 (356[1])	3555 (3960[1])	20.2%	17.52%
South Australia	2748 (2850[7])	927 (1230[7])	3675 (4080[7])	20.9%	12.81%
Queensland	7535 (8106[2])	1161 (1165[2])	8696 (9271[2])	49.4%	22.48%
New South Wales	4677	1253	5930 (6363[3])	33.7%	10.46%
Victoria	2773	820	3593 (4000+[4])	20.4%	2.96%
Tasmania	1627 (1572[5])	570 (717[5])	2197 (2289[5])	13.0%	0.88%
Total Australia	15638	1952	17590	100%	100%

[1] Dunlop *et al.* (1995). [2] Henderson (1997). [3] Harden (1993). [4] Foreman & Walsh (1993).
[5] A.M.Buchanan (1995). [6] Year Book Australia. [7] Haegi (1997).

Under the Cronquist (1981) system adopted to form the framework of this *Flora*, 188 families of dicotyledons, 49 families of monocotyledons, 4 families of pines, 3 families of cycads, 30 families of true ferns and 5 families of fern allies are recognised in the vascular flora of mainland Australia and Tasmania. This includes both native and naturalised taxa, but most families contain at least some native species (exceptions include Betulaceae, Cannabaceae, Papaveraceae and Fumariaceae which in Australia are represented only by naturalised species). The 25 largest families of vascular plants in Australia, approximate numbers of species in each, and the proportion of the flora that they represent are given in Table 3.

Only 23 genera contain 80 species or more. These are listed in descending order in Table 4. About 23% of the Australian vascular flora comes from these 23 genera. The large genera are concentrated in three families, Mimosaceae, Myrtaceae and Proteaceae, which between them contribute about 14% of the vascular flora in 10 genera of 80 species or more. Apart from these three families, only Orchidaceae and Fabaceae have more than one genus with 80 or more species, and they each have only two genera of this size.

Table 3. The 25 largest families of vascular plants in Australia (excluding Island Territories).

Family	Australian genera[2]	Australian species[1, 2]	% of total vascular flora
Myrtaceae	c. 89	c. 1858	9.3%
Fabaceae (*s. str.*)	c. 140	c. 1402	7.0%
Poaceae	219	c. 1302	6.5%
Asteraceae	c. 269	c. 1221	6.1%
Proteaceae	46	c. 1116	5.6%
Mimosaceae	17	994	5.0%
Orchidaceae	98	c. 650	3.3%
Cyperaceae	c. 45	c. 650	3.3%
Epacridaceae	29	c. 424	2.1%
Euphorbiaceae	67	c. 393	2.0%
Goodeniaceae	11	377	1.9%
Rutaceae	41	c. 360	1.8%
Chenopodiaceae	32	302	1.5%
Lamiaceae	38	c. 250	1.3%
Liliaceae (*s. lat.*)	66	266	1.3%
Scrophulariaceae	50	c. 250	1.3%
Myoporaceae	5	238	1.2%
Rubiaceae	42	c. 203	1.0%
Sapindaceae	30	193	1.0%
Solanaceae	23	206	1.0%
Sterculiaceae	23	180	0.9%
Verbenaceae	27	c. 170	0.9%
Apiaceae	36	c. 167	0.8%
Malvaceae	24	c. 165	0.8%
Rhamnaceae	17	c. 160	0.8%

[1] Species numbers are taken from published volumes of *Flora of Australia*, or are ABRS estimates of numbers for unpublished volumes. [2] Note that numbers include both native and naturalised taxa.

Table 4. Genera of Australian vascular plants with 80 or more species.

Genus	No. native species	Family
Acacia	c. 950	Mimosaceae
Eucalyptus s. str.	c. 600	Myrtaceae
Grevillea	352	Proteaceae
Melaleuca	c. 250	Myrtaceae
Eremophila	214	Myoporaceae
Leucopogon	c. 200	Epacridaceae
Cyperus	c. 150	Cyperaceae
Hakea	150	Proteaceae
Stylidium	c. 150	Stylidiaceae
Goodenia	140	Goodeniaceae
Boronia	131	Rutaceae
Olearia	130	Asteraceae
Hibbertia	126	Dilleniaceae
Daviesia	120	Fabaceae
Corymbia	113	Myrtaceae
Pultenaea	112	Fabaceae
Caladenia	c. 104	Orchidaceae
Pterostylis	c. 100	Orchidaceae
Verticordia	100	Myrtaceae
Persoonia	98	Proteaceae
Dryandra	95	Proteaceae
Leptospermum	82	Myrtaceae
Juncus	c. 80	Juncaceae

Previous floristic works on Australia

The first Australian plants named under the binomial system were two species published in 1768 by N.L.Burman. These two plants, mistakenly described as ferns from 'Java', were in fact *Acacia truncata* and *Synaphea spinulosa* from the south-west of Australia. It is thought that they were probably collected by Willem Vlamingh who explored the Swan River in 1697.

The first real insight into the Australian flora, however, came from the large collection of Joseph Banks and Daniel Solander made in 1770. Unfortunately the *magnum opus* planned by Banks and Solander was never published, and their collections were only partly studied by other botanists. Banks encouraged and sometimes sponsored collectors to visit Australia, the most important of these being Robert Brown. Brown's participation in the coastal survey by Matthew Flinders in 1801–1803, and his subsequent stay in New South Wales and Tasmania, resulted in a collection of several thousand species. Brown (1810) commenced a Flora of

Australia (*Prodromus Florae Novae Hollandiae et Insulae Van Diemen*) but the first volume was so disappointingly received, with only a few copies sold, that he never completed the remainder. The *Prodromus*, arranged in a natural system, later came to be recognised as a milestone in taxonomic botany.

Early works on the Australian flora were written and published in Europe, and many were largely accounts of individual collections, e.g. Labillardière (1804–1807) and J.D.Hooker (1855–1860) based chiefly on their own collections, and Lehmann (1844–1848) based on the collections of Ludwig Preiss and to some extent James Drummond.

The Royal Gardens (later Royal Botanic Gardens) at Kew, England, was associated with many early botanical collectors. By the 1850s Kew, under the direction of William Hooker, was becoming a major centre for botanical research. A series of colonial Floras was commenced there, *Flora Australiensis* (1863–1878) by George Bentham being an important contribution to this program. Ferdinand Mueller, the first resident plant taxonomist in Australia, had been keen to write an Australian Flora but was dissuaded by Bentham and Joseph Hooker. They considered that Mueller would be unable to do the work satisfactorily since he could not examine the historical collections housed in European herbaria. Mueller co-operated fully in the preparation of *Flora Australiensis* by sending on loan to Bentham, sequentially over several years, the entire collection of the herbarium in Melbourne (Daley, 1927).

As Government Botanist of Victoria from 1853 to 1896, Mueller developed the herbarium in that Colony into an institution of international importance. He encouraged collectors to travel to many parts of the continent, while he himself collected widely and produced a steady stream of taxonomic publications (for a bibliography of Mueller's works see Churchill, Muir & Sinkora, 1978). Mueller's output has never been approached by later botanists in Australia. From his time onwards, the writing of floristic works on Australia has been carried out chiefly in this country, but with much reliance on the historical material in Europe. This reliance was one of the main factors leading to the establishment of the Australian Botanical Liaison Officer position in Kew in 1937, a position still very relevant today.

Flora Australiensis spawned a number of regional floras, many of which were for the most part extracted from the major work. With time and the great increase in new discoveries, the original work necessary to compile Floras increased, as shown in works such as Black (1922–1929) and Ewart (1930). Floras were produced for all States except Western Australia; that State still has no complete Flora, though it has produced three censuses (Gardner, 1930–1931; Beard, 1965; Green, 1981) and several regional Floras. These original regional Floras have been progressively replaced in recent years by fresh new works generated from research in the State and Commonwealth herbaria. Despite this, there is still a need for the national perspective provided by a continent-wide Flora, and indeed the two types of projects are frequently complementary to each other. Research towards a *Flora of Australia* feeds into the State- and regional-level projects, and *vice versa*, and each product has its own customer base and usage.

Progress of the *Flora of Australia*

The history of this project is described in detail elsewhere in this book, and will not be repeated here.

Volume 1 of the *Flora of Australia* was published in 1981, and by late-1998 twenty one volumes will have been published or be in press. In addition, three volumes of the parallel series *Fungi of Australia* are published, and planning is well advanced on a third series, the *Algae of Australia*. The *Flora* project has also spawned many other publications – 14 of the 15 volumes of the *Australian Flora and Fauna Series* (1984–1991), and seven volumes of the *Flora of Australia Supplementary Series* (1994–). Both series provide, among other things, important bibliographic tools for Australian plant taxonomy.

The revisionary and Flora-writing work funded through the ABRS Participatory Program in association with the *Flora of Australia* project has had a synergistic effect on taxonomic research around the country. Thus many State and regional Floras that would undoubtedly have been written anyway have been facilitated to various degrees, and the research and experience from these have in turn fed back into the national project. Modern State or regional Floras are currently available for much of the country (see *Annotated Bibliography* and *A History of Systematic Botany in Australia*, this volume, for details). However, the greatest single legacy of the *Flora of Australia* project is probably not a book or series of books. It is the increased national awareness engendered among Australia's taxonomic botanists. Few these days would dream of producing a revision of only the taxa found in their own State, whereas only 20 years ago this was the norm. The *Flora of Australia* project, the associated ABRS Participatory Program, and the concurrent forming or blossoming of other national bodies, such as the Council (formerly Committee) of Heads of Australian Herbaria (CHAH) and the Australian Systematic Botany Society (ASBS), have ensured that from now on taxonomic studies on Australia's plants will be undertaken on a continental scale, rather than within artificial political boundaries. This must surely lead to better science.

Conventions and purpose

The *Flora of Australia* will describe all native and introduced Australian vascular plants, bryophytes and lichens. Australian fungi and algae will be described in two parallel series, *Fungi of Australia* and *Algae of Australia*.

The *Flora of Australia* will consist of 59 volumes, some being of more than one part. Volume 1 is an Introduction to the series, providing an overview of the Australian flora, background essays, a general glossary and a key to the families of flowering plants. Volumes 2–48 will describe the vascular plants of the six Australian States, the Northern Territory, the Australian Capital Territory and immediate offshore islands; Volumes 49 and 50 describe the vascular flora of the Australian-administered oceanic islands; Volumes 51–53 will describe the bryophytes of mainland Australia and Tasmania; and Volumes 54–59 will describe the lichens of the same area.

Descriptions and discussion in the *Flora* are concise and supplemented by important references, synonymy, and information on type collections, chromosome numbers, distribution, habitat, and published illustrations. Descriptions are based on Australian material except for some taxa not confined to Australia for which the collections in Australian herbaria are inadequate. Synonymy is restricted to names based on Australian types or used in Australian literature. Misapplied names are given in square brackets together with an example of the misapplication. Alien taxa established in one or more localities, other than under cultivation, are considered naturalised and are included and marked with an asterisk (*). Native species naturalised in parts of the country outside their natural distribution are marked with a hash (#).

Families of flowering plants are arranged in the system of Cronquist (1981). Within each family, genera and species are arranged to show natural relationships, as interpreted by contributors. Although relationships cannot always be shown adequately in a linear sequence, such an arrangement in a *Flora* assists comparison of related taxa. The arrangements adopted for the ferns and gymnosperms, bryophytes, and lichens are described in Volumes 48, 51 and 54 respectively. Keys are provided to genera, species and infra-specific taxa. Up to seven collections are cited for each species and infraspecific taxon.

Maps showing distribution in Australia are arranged in the same sequence as the descriptions, and are grouped together at the end of the main text in each volume. The term 'Malesia' is sometimes used in the notes on geographical distribution for species that occur widely in the region covered by *Flora Malesiana*, i.e. Malaysia, Singapore, Indonesia, the Philippines, New Guinea and adjacent islands.

Line illustrations accompany the descriptions. Usually, these are provided for every genus, and for larger genera a range of species are included. Colour plates supplement the line drawings.

Type citations for taxa below the rank of family are provided in the main body of the text, and for the specimens reflect the authors' understanding of their current status (holotype, isotype, syntype, etc.) and where they are held. In cases where the type specimen has not been examined, this is indicated by *n.v.* These type statements are not to be interpreted as lectotypifications. Where lectotypifications have been made previously, these are cited with *fide*, followed by a reference to the author and place of publication (or, sometimes, to a secondary reference).

New taxa, new combinations and formal lectotypifications are included in an Appendix in the relevant volume, where they are formally published in accordance with the *International Code of Botanical Nomenclature* (Greuter *et al.*, 1994).

Abbreviations, contractions and symbols used in the text are listed after the Appendix. Supplementary glossaries are included in each volume as necessary.

Second Edition of Volume 1

This volume is being compiled 15 years after publication of the first part of *Flora of Australia* (Volume 1, 1st edn), launched at the XIIIth International Botanical Congress in Sydney in August 1981. Since that time about one-third of the planned volumes of the *Flora of Australia* have appeared, with work in progress on about the same number. *Flora of Australia* has been widely recognised internationally as scholarly, authoritative, yet practical and easy to use, among the best of its kind produced anywhere in the world.

The first edition of the *Introduction* was particularly well-received, providing as it did an overview of the history of taxonomic botany in Australia, a review of ideas on the origin and evolution of the Australian flora, a summary of classification schemes, a glossary and a key to the families of Australian flowering plants. It was widely adopted as a university text, and served more widely as a ready reference to the major literature on the Australian flora. It sold out in 1992 and was reprinted in 1993. The reprint itself sold out in 1995. Rather than reprint again, the opportunity has been taken to update the original volume, and to expand the range of review essays presented.

In this second edition we have adopted a completely new structure. The book is intended to provide a primary source of information about the plants of Australia, principally from the point of view of taxonomic botany, but also with relevance to a much wider audience. The first group of essays reviews the history of plant exploration in Australia and its literature, and provides concise biographies of the major collectors and describers of Australia's plants, guides to the location of their collections, and references to more detailed biographies. In the second section two important essays set the context for studies of the Australian flora, with accounts of the present environment, and a review of geological and climatological events of the past which have shaped the physical conditions for the Australian flora. The third section examines the plants themselves, exploring what is known of their fossil history, how they are arranged in communities, what we know of their evolution and biogeography, in both terrestrial and aquatic habitats. The fourth section examines interactions between humans and the flora: the ways in which native plants have been used for food, building materials and implements, ornament, literature and art, and measures currently in place to protect and conserve native plants and vegetation. The essays are followed by a glossary of botanical terms used in the *Flora of Australia*, and a key to families of Australian flowering plants.

Acknowledgments

Many people have co-operated to bring the *Flora of Australia* to fruition. Botanists throughout Australia and overseas have contributed authoritative text, and illustrators have provided line drawings. Each volume contains colour plates from photographs taken by numerous photographers. Additional half-tone photographs include scanning electron micrographs. A feature of the *Flora of Australia* has been the commissioning of watercolour paintings, apposite to the contents, for each volume (except Volume 1, 1st edn). Many individuals have also been involved in refereeing and commenting on the contributions of others. A large number of herbaria, but particularly the Australian State and Federal herbaria represented by the Council of Heads of Australian Herbaria, have contributed hugely to the success of the project, through making their collections freely available to researchers, by providing facilities for research, and by encouraging their staff to participate in the project. Other institutions, particularly universities and State and Federal Government bodies, have also made a major contribution through their specialist staff.

The Australian Biological Resources Study Flora Section has been particularly fortunate over the 23 years of its operation in having as its staff a team of dedicated and enthusiastic scientific editors and flora writers. Their work, carried out in the background, and largely invisible in the final product, has ensured that the *Flora of Australia* enjoys an enviable reputation for consistency, accuracy and presentation. Overlaid on the expertise of our authors and illustrators, it will ensure that the *Flora of Australia* remains the premier source of information on the plants of Australia for decades to come.

In establishing ABRS, the Government wisely instituted a two-layered system of advisory committees. Advising the Minister on policy matters and supervising the ABRS Participatory Program of grants in support of taxonomic work on the biota of Australia, is the ABRS Advisory Committee. On another level, providing advice to ABRS itself, are two further committees, the Flora Editorial Committee (advising ABRS Flora Section) and the Fauna Editorial Committee (advising ABRS Fauna Section). All of these committees draw their members from the wider biological community, providing input to ABRS in terms of community expectations, and professional advice. The outputs of ABRS, both from the grants program and in ABRS publications such as the *Flora of Australia*, are heavily dependent on the contributions of these committee members, and their advice is greatly appreciated.

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A HISTORY OF SYSTEMATIC BOTANY IN AUSTRALIA

A.E.Orchard[1]

Systematic botany is an historical science, in two senses. It was probably the earliest form of botanical study, having its origins in the need to identify useful and dangerous plants. In addition, formal taxonomy requires a depth of knowledge of what has gone before, perhaps more so than in any other science. This knowledge is required, for example, to settle questions of priority of names, and to establish the provenance of particular specimens (particularly Type specimens).

For these reasons, and because the history of science is of interest in its own right, the literature on past taxonomists in Australia is quite large, as are the numbers of botanists and collectors who could be included in an historical survey. The present compilation is necessarily limited in size, and the selection of those included consequently somewhat idiosyncratic. The aim is to provide very brief biographical information on those whose names appear frequently as collectors or authors of Australian plants, with references to more detailed accounts elsewhere. The emphasis is on those associated with the vascular flora, as introductions to the taxonomists and collectors of other groups have been or will be provided for bryophytes in *Flora of Australia* Vols 51 and 53, for lichens in *Flora of Australia* Vol. 54 (Filson, 1992), for fungi in *Fungi of Australia* Vol. 1A (May & Pascoe, 1996) and for algae in *Algae of Australia* Vol. 1. For the most part detailed accounts of living botanists and collectors are not included in this compilation as their history is still being written, although many receive at least a brief mention of their main fields of research.

This work is heavily dependent on various earlier compilations, all of which mention many more individuals than are described here. These works (Maiden, 1908a, 1908b, 1909a, 1909b; J.Willis, 1949a, 1949b, 1949c; Hall, 1978, 1979, 1984, 1989, 1992, 1993; Kraehenbuehl, 1986; Short, 1990a; Willis & Cohn, 1993; Olde & Marriott, 1994) should be consulted for fuller details of the botanists mentioned, and for references to earlier literature, particularly obituaries etc. Many general biographies can also be found in the *Australian Dictionary of Biography* (Melbourne University Press, 1966–). Willis *et. al.* (1986) give birth and death dates and a note on major interests for a large number of collectors and illustrators, and current research is summarised in *Plant Systematics Research in Australasia* (6th edn) (Puttock & Cowley (eds), 1997). A copy of an unpublished compilation of bibliographies of Australian botanists and botanical illustrators, prepared by R.Roberts and M.Whitten for the Hunt Botanical Library, Pennsylania, U.S.A., in the 1980s provides some additional information, and is housed in the Australian National Herbarium (CANB). Here and subsequently herbarium acronyms follow Holmgren *et al.*, *Index Herbariorum Part 1: The Herbaria of the World* (1990)).

In general the references cited in this chapter have been chosen because they are reasonably accessible. The list is by no means comprehensive. Wherever possible, herbaria holding relevant collections are cited. These are taken from Stafleu & Cowan, *Taxonomic Literature* Vols 1–7 (1976–1988) and *Supplements* by Stafleu & Mennaga (1992–1995), from Holmgren *et al.*, *Index Herbariorum Part 1: The Herbaria of the World* (1990), from *Index Herbariorum Part II Collectors* (1954–1988), and from personal knowledge. *Taxonomic Literature* and its *Supplements* also provide valuable supplementary biographical notes, as well as additional references.

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Western Australia

The first herbarium specimens from Australia were collected by William Dampier in Western Australia in 1699 (or perhaps by Willem de Vlamingh in 1697). These, along with most other specimens collected over the next 200 years (Baxter, Brown, Cunningham, Diels & Pritzel, Drummond, Fraser, Gaudichaud, Hügel, Labillardière, Leschenault, Maxwell, Menzies, Mueller, Preiss) found their way to collections outside the State. In the mid- to late-1890s the Museum & Art Gallery is believed to have started a small herbarium under its Director, Bernhard Henry Woodward (1846–1916). At about the same time Alexander Morrison was appointed botanist in the Bureau (later Department) of Agriculture, and began assembling an herbarium, probably largely centred around his interest in poisonous plants. Morrison was retrenched in 1906, and died in 1912, bequeathing his private collection to EGH (now E), the official collection staying with the Department. In 1911 Morrison was replaced by Frederick Stoward, who continued to build the official collection until 1917. Stoward's private herbarium is now to be found in BM, K and MEL. The Department of Agriculture Herbarium was in the care of Desmond Andrew Herbert from 1918 until 1921.

The Conservator of Forests had announced the establishment of a forestry herbarium in 1916, which in 1920 employed Charles Gardner as collector. In 1924 Gardner transferred to the Department of Agriculture, being designated Government Botanist and Curator from 1929. Under his guidance the Agriculture and Forestry herbaria were merged in 1928, and the Museum Herbarium was added in 1957–1960. On 1 July 1988 the combined Western Australian Herbarium was transferred to the Department of Conservation and Land Management.

Gardner remained Government Botanist until 1960, being succeeded as Curator by Robert Royce (1960–1974). Subsequent Directors were John Green (1975–1987), Bruce Maslin (Acting, 1988–1989), Jim Armstrong (1989–1992) and Neville Marchant (1992–).

Physically, the Western Australian Herbarium (PERTH) was housed in the old Observatory Building until 1959, when it moved to the Department of Agriculture Head Office site at Jarrah Rd, Kensington. In 1970 the herbarium moved to a purpose-built building on the Kensington site.

The Botany Department at the University of Western Australia established an herbarium (UWA) in 1914. At its height it contained about 20 000 specimens, particularly those of B.J.Grieve. The vascular plant and fungal specimens of research value were transferred to PERTH in about 1988.

Since 1962, Kings Park and Botanic Gardens (KPBG) has maintained a small reference herbarium (currently just over 25 000 specimens) in association with the living collections. Duplicates of most wild-collected specimens are in PERTH.

In recent years many Western Australia-based botanists have contributed to knowledge of the Australian flora. Notable among these are Jim Armstrong (Rutaceae, pollination biology), Eleanor Bennett (Myrtaceae, Proteaceae), Norman Brittan (*Thysanotus*), Jenny Chappill (*Andersonia*, *Jacksonia*, Sterculiaceae), Richard Cowan (Caesalpiniaceae, Fabaceae, Mimosaceae), Alex George (Caesalpiniaceae, Myrtaceae, Orchidaceae, Proteaceae), John Green (Myrtaceae), Steve Hopper (*Anigozanthos*, *Conostylis*, *Eucalyptus*), Kevin Kenneally (Kimberley flora), Nicholas Lander (Malvaceae, *Olearia*), Terry Macfarlane (Fabaceae (especially *Pultenaea* group), *Haemodorum*, *Lomandra*, Poaceae, *Wurmbea*); Neville Marchant (Droseraceae, Myrtaceae, Xyridaceae), Bruce Maslin (*Acacia*), Gillian Perry (Loganiaceae, naturalised flora), Barbara Rye (Rhamnaceae, Thymelaeaceae), Judy Wheeler (*Hibbertia*, regional Floras) and Paul Wilson (Asteraceae, Chenopodiaceae, Rutaceae).

Western Australia has never had a State-wide Flora. In 1952 Gardner published the first part of a proposed State Flora (Gramineae) but no further parts appeared. Several regional Floras are available. In 1954 the first part of *How to Know Western Australian Wildflowers* by W.E.Blackall & B.J.Grieve appeared. This illustrated key to the plants of the South West and southern Eremaean Provinces has since appeared in many parts and several editions. In 1987 the Western Australian Herbarium published the 2-volume *Flora of the Perth Region*

(N.G.Marchant *et al.*), covering the coastal plain and escarpment, with full descriptions, distributions and ecological notes. In a similar style, *The Flora of the Kimberley Region* (J.R.Wheeler (ed.) *et al.*) was published by the Herbarium in 1992. The arid zone is covered by *Flora of Central Australia* (ed. J.P.Jessop, 1981). A *Census of the Vascular Plants of Western Australia* was published by J.W.Green (1981), with a second edition in 1985 and a number of updates in subsequent years. The journal *Nuytsia* was established by the Western Australian Herbarium in 1970 to publish taxonomic papers on the Western Australian flora. It has appeared irregularly ever since, with about two issues per year in recent years. In 1988–1990 the Herbarium produced another occasional series, *Kingia*, to publish non-taxonomic papers on the vegetation and flora of Western Australia. It replaced the earlier *Western Australian Herbarium Research Notes*, of which 12 parts appeared between 1978 and 1986. The function of *Kingia* was absorbed by *CALMScience* from 1990. Kings Park also has an occasional journal, *Kings Park Research Notes*, first published in 1973.

References: Gardner, 1947; Keighery, 1978; Maslin, 1988a; Green, 1990.

Northern Territory

Despite visits by several Dutch ships early in the 17th century, the first scientific collections from the Northern Territory were not made until Robert Brown landed in eastern Arnhem Land in 1803, during Flinders' *Investigator* voyage.

From then until the 1950s botanical exploration of the Northern Territory was undertaken by visiting expeditions, or by a handful of residents who sent specimens to New South Wales, Victoria, South Australia or overseas for study. Allan Cunningham collected in coastal parts of north-western Arnhem Land during Philip King's voyages of 1818–1821. John Armstrong was a resident collector for Kew at Port Essington from about 1838, while John MacGillivray visited in 1844 and 1848. Ludwig Leichhardt collected in Arnhem Land in 1845, and Mueller collected around the Victoria River and elsewhere on the Gregory Expedition of 1855–1856. Diedrich Henne (1834–?), botanist on the Landsborough Expedition of 1861–1862 in search of Burke and Wills, collected in the Gulf of Carpentaria and along the Albert River. His collections went to Mueller (MEL). John McDouall Stuart made collections from inland Northern Territory during his trans-Australian expedition of 1862. The brothers T.A. & B.Gulliver collected at Caledon Bay, Liverpool River and Castlereagh Bay in 1867, sending their collections to Mueller (MEL). Further small collections were made by F.Cadell (Liverpool River, 1867), Maurice Holtze (Croker Island, Mountnorris Bay, 1883, specimens in AD), M.W. & N.Holtze (East Alligator River, 1886, specimens in MEL), N.B.Tindale (Groote Eylandt and Ross River, 1921–1922, specimens in NSW), G.H.Wilkins (Crocodile Islands, Groote Eylandt, 1924–1925, specimens in BM), H.Basedow (Arnhem Land, 1928, specimens in K and AD) and Donald F.Thompson (eastern Arnhem Land, 1935–1937, specimens in BRI and UMEL).

A major expedition to Arnhem Land was mounted in 1948, jointly sponsored by the National Geographic Society, the Smithsonian Institution and the Commonwealth Government. The results of this expedition were published by Specht & Mountford (1958).

The CSIRO Division of Land Use Research (later, Land Research and Regional Survey Section) north Australian surveys (1946–) produced many specimens, from widely distributed localities throughout tropical Australia. These specimens formed the basis of the present CANB herbarium. In particular, the 1972–1973 survey of the Alligator Rivers region (which includes the present Kakadu National Park) was significant in discovering a rich endemic flora in the sandstone plateau of western Arnhem Land.

Until self-government in 1978, collecting and institutions in the Territory were under Commonwealth Government control. In 1954 a Botany Section and Herbarium (NT) within the Animal Industry Branch of the Northern Territory Administration (Department of Territories) was established at Alice Springs under the direction of George Chippendale, with a single technician, Des Nelson. Chippendale left in 1966, being replaced by John

Maconochie in 1967. In 1968 the herbarium was relocated to the Arid Zone Research Institute, 10 km south of Alice Springs. In 1966 a second herbarium was established in Darwin, in the charge of Norm Byrnes, and this herbarium (DNA) in 1989 absorbed most of the collections of NT, leaving the latter as a small reference collection. In 1983 the two Northern Territory herbaria were transferred from the Department of Primary Production to the Conservation Commission of the Northern Territory (now Parks and Wildlife Commission of the Northern Territory). The Darwin herbarium was relocated to Palmerston, a satellite town outside Darwin, in 1989. The Northern Territory Herbarium (DNA) was administratively merged with the Darwin Botanic Gardens in late 1994, although it remained physically at Palmerston. The Chief Botanist for the merged institution is Greg Leach.

In recent years research on the plants of the Northern Territory has been carried out by David Albrecht (Campanulaceae, *Monotoca*), Ian Cowie (*Polycarpaea*, Sterculiaceae), Clyde Dunlop (Asteraceae, *Mitrasacme*), Peter Latz (ethnobotany, Cyperaceae), Greg Leach (*Acacia*, Elatinaceae, Eriocaulaceae), John Maconochie (*Acacia, Cycas*, Fabaceae, *Hakea*), Bruce Thomson (*Euphorbia*) and Glenn Wightman (ethnobotany, mangroves).

In 1917 Ewart & Davies published *The Flora of the Northern Territory*, the only complete Territory Flora produced so far, although a *Check List of Northern Territory Plants* (G.M.Chippendale) was produced in 1972, and this was superseded by *Checklist of the Vascular Plants of the Northern Territory, Australia* (C.R.Dunlop *et al*., 1995). In 1958 R.L.Specht & C.P.Mountford (eds) published the botanical results of the 1948 *American–Australian Scientific Expedition to Arnhem Land*. The arid half of the Territory was covered by *The Flora of Central Australia* (J.P.Jessop (ed.), 1981), and work is underway on a 4-volume *Flora of the Darwin Region* (C.R.Dunlop, G.J.Leach & I.D.Cowie), of which Volume 2 appeared in 1995. An *Atlas of the Vascular Rainforest Plants of the Northern Territory* (D.T.Liddle *et al*.) was published in 1994. An occasional series of monographs, *Northern Territory Botanical Bulletin*, was established in 1976, and contains papers on taxonomy, ethnobotany and conservation.

References: Maiden, 1908c; Specht & Mountford, 1958; Anonymous, 1979b; Mitchell, 1980.

Many of the botanists and collectors discussed under South Australia, and some from the other States, also collected or had expeditions within the Northern Territory. In particular, see Eardley, Forrest, Giles, Gosse, Helms, Leichhardt, Mueller and Tate.

South Australia

A Botanic Garden was established on the banks of the River Torrens in 1839, under the direction of John Bailey (Bailey, 1891). It was mainly devoted to providing fresh produce for the young colony, and was closed about 1841 (White, 1949). The present Botanic Gardens was established in 1855 with G.W.Francis as Superintendent (1855–1860), later Director (1860–1865) (see Best, 1986).

The earliest herbarium in South Australia, of Australian and overseas plants, was assembled by R.Schomburgk, Director of the Adelaide Botanic Gardens (1865–1890). This was donated to the University of Adelaide in the 1930s, where it joined other herbaria assembled by R.Tate, J.G.O.Tepper, and J.M.Black. The first botanical library, also assembled by Schomburgk, was donated to the Public Library in 1932.

An herbarium was established at the Botany Department, University of Adelaide, by Tate, and this was subsequently enhanced by collections from several of the early exploring expeditions, and by those of J.M.Black, J.B.Cleland, M.Koch, A.Morris, R.S.Rogers and others. The Curator of the University Herbaria at the Botany Department and at the Waite Agricultural Research Institute (ADW) from 1933–1949 was C.M.Eardley.

A new State Herbarium was established in the Adelaide Botanic Garden under the Directorship of Noel Lothian in 1953. From 1953 to 1954 it was under the acting Keepership of Ted Booth. Booth had previously been an honorary assistant in the University Herbarium.

In 1955 Hansjoerg Eichler was appointed first permanent Keeper, and under his direction the collections of the University of Adelaide were transferred to the State Herbarium of South Australia (AD) on permanent loan. In 1957 the South Australian Museum collection was also transferred to AD.

Over the next 20 years Eichler developed a network of collectors throughout the State, and established a gradually expanding staff and purpose-built building (from 1965): by 1990 AD held about 700 000 specimens. He developed close links with the University of Adelaide, stimulating taxonomic research as a postgraduate option. The Botanic Gardens already had a substantial library, and this was rapidly expanded. Eichler was succeeded by John Jessop in 1975 as Chief Botanist. In 1989, following the retirement of Bryan Womersley from the Botany Department, University of Adelaide, the ADU algal collections (totalling about 80 000 specimens, 4000 wet collections and 11 000 slides) were also transferred to AD. Important suites of collections in AD, apart from those already mentioned, are those of C.R.Alcock, A.M.Ashby, A.C.Beauglehole, B.J.Copley, N.N.Donner, D.Hunt, E.H.Ising, E.N.S.Jackson, D.N.Kraehenbuehl, A.G.Spooner and D.J.E.Whibley, and specimens from a number of the early exploring expeditions (Basedow, Calvert, Elder Exploring Expedition, Horn, Madigan and Tietkens) received via ADU.

An herbarium had existed at the Waite Institute since 1930, under the care of C.M.Eardley (1933–1949), G.H.Clarke (1936–1939), N.T.Burbidge (1943–1946), E.L.Robertson (1948–1953), F.M.Hilton (1953–1955) and D.E.Symon (1957–1985). The emphasis of this herbarium was largely on weeds, but general native collections were also incorporated. Important collections included those of A.Morris from the Broken Hill region, and those of D.E.Symon (Australia-wide). An arboretum was developed at the Waite Institute as an adjunct to the herbarium. The ADW collection had reached about 55 000 sheets in 1985, when the decision was made to close it down, and transfer the specimens to AD.

Major revisionary work carried out in association with the South Australian herbaria includes that of Bill Barker (*Hakea*, Scrophulariaceae, Stackhousiaceae), Robyn Barker (Acanthaceae, *Hakea*, Malvaceae, Zygophyllaceae), Bob Bates (Orchidaceae), John Carrick (*Prostanthera*, carried on after his death by Barry Conn), Bob Chinnock (ferns, Myoporaceae), John Conran (Commelinaceae, Malvaceae), Hansjoerg Eichler (Apiaceae, Ranunculaceae, Zygophyllaceae), Laurie Haegi (*Hakea*, Solanaceae), A.A.Munir (Verbenaceae), Tony Orchard (*Acaena*, Haloragaceae), Richard Schodde (Atherospermataceae, *Millotia*), Elizabeth Shaw (Brassicaceae), David Symon (*Cassia*, *Solanum*, other Solanaceae), Helmut Toelken (Crassulaceae, *Hibbertia*, *Kunzea*), Joe Weber (*Cassytha*, *Thelymitra*), David Whibley (*Acacia*), Paul Wilson (Rutaceae) and Bryan Womersley (marine algae).

South Australia was among the first in the country to have a comprehensive State Flora. After an initial effort by Tate (*A Handbook of the Flora of Extratropical South Australia*, 1889), Black produced his 4-volume *Flora of South Australia* in 1922–1929, with a second edition in 1943–1957 (the last part completed by Enid Robertson), Eichler produced a major *Supplement* in 1965, and J.P.Jessop & H.R.Toelken edited a multi-author third edition in 1986. An updated census *A List of the Vascular Plants of South Australia, Edition IV* (J.P.Jessop, ed.) was produced in 1993. In addition J.P.Jessop edited a *Flora of Central Australia* in 1981. In 1983 B.D.Morley & H.R.Toelken coordinated and edited production of a major overview volume, *Flowering Plants in Australia*. Since 1976 the State Herbarium has published a taxonomic journal, *Journal of the Adelaide Botanic Gardens*.

References: Lothian, 1949; Symon, 1974, Jessop, 1978; Symon, 1985; Best, 1986; Womersley & Jessop, 1989; Barker, 1998.

Queensland

The Moreton Bay district was settled in 1824 as part of New South Wales, Queensland becoming a separate colony in 1859. Walter Hill was appointed Superintendent of the Brisbane Botanic Gardens in 1855. He became Colonial Botanist and Curator of the Botanic Gardens in 1859, until his retirement in 1881. His main interest was in economic botany, although he had some contact with Mueller (MEL) and W.J.Hooker (K). He developed a small herbarium, most of which was subsequently destroyed by termites and damp, and began development of the present Queensland Herbarium library.

Hill was succeeded by F.M.Bailey as Colonial (later, Government) Botanist (1881–1915). He laid the foundations of the current herbarium by bringing with him his large personal collection. On his retirement, his son J.F.Bailey became Government Botanist and Curator of the Brisbane Botanic Gardens for 18 months in 1905–1906, before being succeeded himself by F.M.Bailey's grandson, C.T.White. White was Government Botanist from 1907–1950, being succeeded by W.D.Francis (1950–1954), S.L.Everist (1954–1976), R.W.Johnson (1976–1990) and G.P.Guymer (1990–).

From 1879 until 1889 the herbarium was in the basement of the Queensland Museum in Queen Street. In 1889 it was linked with a Museum of Economic Botany, and together they occupied about 80% of a new building in William Street constructed for the Department of Agriculture. In 1912 a new building was erected for the Botanic Museum and Herbarium adjacent to the Botanic Gardens. The building was shared with the Government Entomologist and Plant Pathologist, and much of the space was occupied by the Museum of Economic Botany. In 1968 a new Botany Building was constructed in the Indooroopilly complex of the Department of Primary Industries. In 1992 the Queensland Herbarium was transferred from the Department of Primary Industries to the Department of Environment & Heritage, although it remained on the Indooroopilly site. Recently, the circle was completed when the Queensland Government opened a new herbarium facility on the Botanic Gardens site at Mt Coot-tha on 6 May 1998.

The Department of Botany at the University of Queensland maintained a teaching herbarium (BRIU) from 1940–1990. The majority of the collections were made by D.A.Herbert and A.B.Cribb in the 1950s. The fungal specimens from this herbarium were transferred to BRIP in about 1980, the algal specimens to BRI in 1989, the angiosperm collections (about 3500 sheets) to BRI, QRS, MEL and the Gympie Forestry school in 1990, and the lichen collections (about 20 000 specimens, mainly collected by R.W.Rogers, C.Scarlett and G.N.Stevens) to BRI in 1991.

A number of herbaria have also been developed in northern Queensland. Hugo Flecker founded the North Queensland Naturalists' Club in Cairns in 1932. This club developed a local herbarium (CAIRNS) of about 11 000 specimens. The vascular plants from this herbarium were transferred to QRS in 1971, with the bryophytes going to CANB in 1981.

In 1979 the Queensland Herbarium established a field station at Mareeba, and a regional herbarium (MBA) of about 8000 specimens has been built up there under the direction of John Clarkson (Rubiaceae, far northern Queensland flora). It specialises in plants of northern Queensland, particularly Cape York Peninsula, and duplicates of most MBA specimens are held in BRI.

The CSIRO established an outpost herbarium at Atherton (QRS) in 1971. This herbarium, under the direction of Bernie Hyland (Australian rainforest trees), now holds about 100 000 specimens, mainly of northern Queensland rainforest trees. Duplicates of many of these specimens are held in BRI and CANB.

The Botany Department of James Cook University has since 1961 maintained a small herbarium (JCT), comprising about 22 000 specimens including the algal collection of 10 000 specimens by Ian Price. The director is Betsy Jackes (Myrsinaceae, Vitaceae). The herbarium contains northern Queensland vascular plants (Jackes), marine algae (Ian Price) and fungi (Warren Shipton).

Apart from the historical figures discussed below, major taxonomic work on the Queensland vascular flora has been carried out in recent times by Peter Bostock (ferns), Trevor Clifford (family delimitation in Liliaceae complex), Paul Forster (Apocynaceae, Asclepiadaceae, Euphorbiaceae), Gordon Guymer (Myrtaceae, Sterculiaceae, Winteraceae), David Halford (*Hedyotis*, Tiliaceae), Rod Henderson (*Dianella*, Euphorbiaceae), Ailsa Holland (Asteraceae, Fabaceae, *Trachymene*), Laurie Jessup (Annonaceae, Ebenaceae, Flacourtiaceae, Sapotaceae, Symplocaceae), Bob Johnson (Convolvulaceae, Cuscutaceae), Les Pedley (*Acacia*, Fabaceae, Polygalaceae), Sally Reynolds (Rubiaceae, Sapindaceae) and Bryan Simon (Poaceae).

The most recent complete Flora of the State is *The Queensland Flora*, published in six volumes plus index by F.M.Bailey (1899–1902, 1905). A *Comprehensive Catalogue of Queensland Plants Both Indigenous and Naturalised* was written by Bailey in 1913. A further census (*Queensland Vascular Plants. Names and Distribution*, R.J.F.Henderson, ed.) was published in 1993, and between 1983 and 1989 a multi-author 3-volume *Flora of South-Eastern Queensland*, edited by T.D.Stanley & E.M.Ross, was published. The Queensland Herbarium issued an occasional series of botanical monographs under the title *Contributions from the Queensland Herbarium* (Nos 1–20) between 1968 and 1977. From 1977 this series was renamed *Austrobaileya*.

References: White & Blake, 1947; Flecker, 1950; Herbert, 1959; Everist, 1982; Forster & Jessup, 1990.

New South Wales

Australia's first farm, nine acres of corn, was established at Farm Cove on Sydney Harbour in 1788. Later, on 13 June 1816, the Sydney Botanic Gardens was founded on the same site by Governor Macquarie, as part of the Governor's Domain. The first Colonial Botanist and Superintendent of the Gardens was Charles Fraser, from 1817 (formally appointed 1821). Fraser died in 1831, and was succeeded by his assistant John McLean (1831–1833) and Richard Cunningham (1833–1835). John McLean was Acting Superintendent in 1836, before Allan Cunningham briefly succeeded his brother (1837). Later Superintendents included James Anderson (1838–1842), Naismith Robertson (1842–1844) and James Kidd (1844–1847). In 1847 John Carne Bidwill was appointed first Director, followed in 1848 by Charles Moore. Moore was appointed on the recommendation of John Lindley, and held the position until 1896. It was during this period that the gardens developed its present form. A small herbarium was apparently in existence from about 1853, and Maiden (1908a) mentions that William Vernon was in charge of it in 1857 during F.Mueller's visit to Sydney. This herbarium was undoubtedly used by Charles Moore and Ernst Betche in producing their *Handbook of the Flora of New South Wales* in 1893.

The development of the existing herbarium (NSW), however, essentially dates from 1896, when J.H.Maiden was appointed Government Botanist and Director of the Botanic Gardens. Maiden remained in this position until 1924, being succeeded by Percy Darnell-Smith (1924–1933). The Gardens and Herbarium administrations were separated in 1933, with the Herbarium Curators being Edwin Cheel (1933–1936) and Robert Anderson (from 1936). The reunification of the two posts occurred under Anderson (1945–1965), subsequent Directors of the Royal Botanic Gardens being Knowles Mair (1965–1970), John Beard (1970–1972), Lawrence ('Lawrie') Johnson (1972–1985), Carrick Chambers (1985–1996) and Frank Howarth (1996–). Maiden established a firm tradition of high quality taxonomic work at the Sydney herbarium, particularly in the genera *Eucalyptus* and *Acacia*. This tradition of studying Australia's iconic genera has been followed by other staff at NSW. In the case of *Eucalyptus* this has involved Don Blaxell, Ken Hill and Lawrie Johnson. Studies on other genera of Myrtaceae have been carried out by Barbara Briggs, Lawrie Johnson, Joy Thompson and Peter Wilson. Australia's other great genus, *Acacia*, has been the subject of study by Mary Tindale, who is well known for her work on other groups as well, including the ferns. In recent years the NSW herbarium has also taken a leading role in studies on monocotyledons, particularly Cyperaceae (Karen Wilson), Juncaceae (Lawrie Johnson, Karen Wilson), Restionaceae (Barbara Briggs, Lawrie Johnson), Xanthorrhoeaceae (Alma Lee, David Bedford) and Xyridaceae (Barry Conn). Proteaceae have been another focus of research, with landmark studies by Briggs and Johnson, and more recent work by Don

McGillivray and Peter Weston. Other major studies have been undertaken on Araceae (Alistair Hay), Casuarinaceae (Lawrie Johnson, Karen Wilson), Epacridaceae (Elizabeth Brown, Jocelyn Powell), Lamiaceae and Loganiaceae (Barry Conn), legumes (Joy Thompson, Mary Tindale, Peter Wilson), Poaceae (Joy Everett, Surrey Jacobs, Joyce Vickery), freshwater vascular plants (Surrey Jacobs), gymnosperms (including cycads) (Ken Hill). Cryptogamic groups have been studied by Alan Archer (lichens), Elizabeth Brown (liverworts), Valerie May (algae), Alan Millar (marine algae), Helen Ramsay (mosses) and Mary Tindale (ferns).

The collections at NSW currently amount to about 1 million specimens, of which 60% are Australian flowering plants. There are sizeable collections of bryophytes, lichens and algae, but fungal collections were transferred to DAR in the early 1970s. An overview of the bryophyte and lichen collections was provided by Ramsay & Briggs (1979). For many years NSW has employed official collectors (E.F.Constable, R.Coveny, A.N.Rodd) who have gathered very large numbers of collections, including duplicates distributed world-wide.

In 1939 the series *Contributions from the New South Wales National Herbarium* was established to publish taxonomic papers. Four volumes (in several parts each) were published from 1939–1973, when the journal was renamed *Telopea* (1975–) and issued in slightly different format. In 1961 a parallel series of publications, *Contributions from the New South Wales National Herbarium: Flora Series* (1961–1974) was published to make available State-wide monographs. A total of 211 parts was published before it was renamed *Flora of New South Wales*. This latter monographic series was incomplete when it was abandoned in 1984, in favour of a 4-volume handbook, *Flora of New South Wales* (1990–1993) produced under the editorship of Gwen Harden. The National Herbarium of New South Wales has since 1981 also published the journal *Cunninghamia*, which contains ecological and biogeographical papers on New South Wales flora.

Three other sizeable vascular plant herbaria are active in New South Wales. The Beadle Herbarium of the University of New England, Armidale (NE), holding about 50 000 specimens, has been the base for N.C.W.Beadle, as well as for John Williams (studies in rainforest plants) and Jeremy Bruhl (Anthemideae (Asteraceae), Cyperaceae, Euphorbiaceae). This herbarium moved into a new purpose-built wing on 20 June 1997. The Herbarium of the Botany Department of the University of Sydney (SYD) was established in 1914. It has been curated by Obed Evans (1916–1954), Roger Carolin (1955–1989, noted for work on Geraniaceae and Goodeniaceae, in particular) and by Murray Henwood (1990–, Apiaceae, Araliaceae). The John T. Waterhouse herbarium at the School of Botany, University of New South Wales (UNSW) was established in 1960 and curated by John Waterhouse until his death. It is currently curated by Chris Quinn (Sapindales, gymnosperms).

In addition to the 4-volume *Flora of New South Wales* (1990–1993), five regional Floras are available for New South Wales and the Australian Capital Territory: *Flora of the* A.C.T. by N.T.Burbidge & M.Gray (1970), *Student's Flora of North Eastern New South Wales* (1971–1987) by N.C.W.Beadle; *Kosciusko Alpine Flora* by A.B.Costin, M.Gray, C.J.Totterdell & D.J.Wimbush (1979), *Plants of Western New South Wales* (1981) by G.M.Cunningham, W.E.Mulham, P.L.Milthorpe & J.H.Leigh, and *Flora of the Sydney Region* (4th edn) by R.C.Carolin & M.D.Tindale (1993).

References: Froggatt, 1932; Anderson & Vickery, 1947; Evans, 1950; Hyams, 1969; Carolin, 1975; Briggs, 1976; Ramsay & Briggs, 1979; Gilbert, 1981; Briggs, 1982; Finney, 1984; Gilbert, 1986; Russell-French, 1997.

Australian Capital Territory

The Australian Capital Territory, an enclave within New South Wales, has also had active herbaria for many years. The Forest Research Institute herbarium (FRI) was established in 1927 in the Australian Forestry School. Its first botanist was R.D.Johnston (1951–1969). George Chippendale joined the staff in 1966, and was director 1966–1983. Ian Brooker was also a member of staff from 1970. In 1975 the Forest Research Institute became the CSIRO Division of Forest Research. Herbarium FRI at its peak contained over 20 000 specimens, about three quarters of them *Eucalyptus*. It held many Blakely duplicates from NSW (including isotypes), a set of 123 duplicates of Robert Brown, and Allan Cunningham duplicates from BM, received in 1974. It is now associated with CANB, which houses the former FRI *Eucalyptus* collection.

After recommendations from Dr Arthur Hill in 1926, CSIRO established an herbarium (CANB) under the direction of J.Calvert in 1930. Known as Herbarium Australiense (as 'Australiensis' at first) this collection grew slowly until the appointment of Nancy Burbidge in 1946 as the first fulltime systematic botanist. Burbidge was employed by the Division of Plant Industry, CSIRO, but parallel work was being undertaken (and a parallel collection assembled) in the CSIRO Division of Land Use Research. These two herbaria were united in 1973. The combined herbarium was equipped with an extensive library, thanks to the influence of Ru Hoogland in the 1950s and 1960s. This library was further enhanced by Burbidge's successor as curator, Hansjoerg Eichler. More recently the herbarium has been under the direction of Bryan Barlow, followed by Judy West.

In 1984 FRI was administratively linked to CANB, although the two still operate as separate units. The CSIRO established an outpost herbarium at Atherton (QRS) in 1971. This herbarium, of about 100 000 specimens, mainly of northern Queensland rainforest trees, operates as a branch of CANB under the direction of Bernie Hyland (rainforest trees, particularly Lauraceae, Sterculiaceae). In 1984 CANB had its name officially changed to Australian National Herbarium.

Another herbarium (CBG) was established at the Australian National Botanic Gardens (ANBG) in Canberra in 1945. Initially established to service the identification and vouchering requirements of the ANBG native plant collections, it subsequently developed a research function as well. It was under the direction, successively, of Marie Phillips, Arthur Court (*Acacia*), Jim Armstrong (Rutaceae, pollination biology) and Jim Croft. In 1993 this herbarium merged with CANB to form the core of the Centre for Plant Biodiversity Research (CPBR), a cooperative venture between CSIRO and the then Australian Nature Conservation Agency (ANCA, now part of Environment Australia, Department of Environment and Heritage). This united herbarium (CANB) now holds about 750 000 specimens, and is national in scope.

From about 1970, Professor J. (Jack) A. Elix developed an herbarium of lichens at the Department of Chemistry, Australian National University (ANUC). At its height it contained c. 40 000 specimens. From 1995 to 1997 about 30 000 of these were transferred to CANB, and the remainder will eventually follow.

Another herbarium (GAUBA) was established at the Australian National University by Professor L.D.Pryor in 1958, based largely on collections made by him and Erwin Gauba. It was intended principally for teaching purposes, and currently is housed in the Division of Botany and Zoology under Michael Crisp. It contains about 25 000 specimens, mainly of Australian vascular plants.

Botanists from the Australian Capital Territory who have made recent contributions to Australian taxonomy include Laurie Adams (Asteraceae, Caryophyllaceae, Gentianaceae), Bryan Barlow (Loranthaceae, *Melaleuca*, Viscaceae); Doug Boland (*Eucalyptus*), Ian Brooker (*Eucalyptus*), Mark Clements (Orchidaceae), Arthur Court (*Acacia*), Lyn Craven (Chamelaucieae, *Heliotropium*, Malvaceae, *Melaleuca*), Mike Crisp (Fabaceae, Proteaceae), Max Gray (Asteraceae, alpine flora), Tom Hartley (Myrtaceae, Rutaceae), Helen Hewson (Brassicaceae and many other families in *Flora of Australia*), David Jones (cycads, ferns, Orchidaceae, palms), Mike Lazarides (Poaceae), Bob Makinson (*Astrotricha*, *Grevillea*), Ted Moore (*Senna*), Jo Palmer (Amaranthaceae), Chris Puttock (Asteraceae), Heinar Streimann (mosses); Ian Telford (Cucurbitaceae, rainforest families), Kevin Thiele and Frank Udovicic (Rhamnaceae), Doug Verdon (lichens), Les Watson and collaborators (interactive databases at family level, Poaceae), Carolyn Weiller (nee Mihaich) (Poaceae) and Judy West (Caryophyllaceae, *Dodonaea*, Portulacaceae).

A regional flora is available for the Australian Capital Territory: *Flora of the A.C.T.* by N.T.Burbidge & M.Gray (1970), and all Australian Capital Territory plants are included in G.Harden (ed.), *Flora of New South Wales* (1990–1993).

References: Hartley, 1947; Chippendale, 1976; Wrigley, 1980; Barlow, 1984.

Victoria

The first botanical descriptions of the vegetation of Victoria were those of Caley in 1801, Leschenault in 1802, and Fleming in 1803 (for details see Ducker, 1991; Willis & Cohn, 1993). None of these botanists appears to have made collections. The first collections were made in Port Phillip Bay by Ferdinand Bauer, Robert Brown and Peter Good during Flinders' *Investigator* voyage in 1802, and Brown again visited Port Phillip in 1804. Subsequent visitors to the southern coast included William Baxter and Jules Dumont d'Urville, both in 1826, James Backhouse in 1827 (Willis & Cohn, 1993) and Ronald Gunn in 1836 (Ducker, 1991). Overland explorers included Hume and Hovell in 1824–1825 (no collections), Johann Lhotsky in 1834, and Thomas Mitchell in 1836 (Willis & Cohn, 1993). Botanical exploration in the 1840s was sparse but is summarised by Willis & Cohn (1993).

Melbourne's Botanic Gardens was established in 1846 by the Superintendent of the Port Phillip District, Charles La Trobe, with John Arthur and John Dallachy as Superintendents. In January 1853 Ferdinand Mueller was appointed first Government Botanist in 1857, and subsequently Director of the Botanic Gardens. He immediately undertook extensive collecting expeditions throughout Victoria and southern New South Wales, and gradually built up an extensive, Australia-wide network of collectors and correspondents. During the next 43 years Melbourne and Mueller became synonymous with taxonomic botany in Australia. Specimens from most of the great 19th century exploring expeditions were sent to Melbourne, including those of Babbage, Burke and Wills, J. and A.Forrest, Giles, Gregory, Howitt, Lindsay, McDouall Stuart and Tietkens. These, plus Mueller's own collections and those of his correspondents, laid the foundation of what is today Australia's largest and historically most important herbarium (MEL).

On Mueller's death the herbarium was somewhat neglected for the earlier part of this century. J.G.Luehmann succeeded Mueller as Government Botanist 1896–1904. A.J.Ewart was appointed Government Botanist (1905–1921) but was simultaneously Professor of Botany at the University of Melbourne, a duty which occupied much of his time, and which led to him relinquishing the Government Botanist position. The publication of Ewart's *Flora of Victoria* (1931) marked the beginning of the revival of MEL's fortunes. The position of Director of the Botanic Gardens was linked to that of Government Botanist in subsequent years, incumbents being Alexander W.Jessep (1941–1957), Richard T.M.Pescott (1957–1971) and David M.Churchill (1971–1985). From 1985 the Director and Government Botanist positions were replaced by Managers. In 1991 the Victorian Government passed the Royal Botanic Gardens Act, which removed the Gardens from the Public Service to the control of a Board. The present Director is Philip Moors.

At first the Melbourne herbarium was housed in a small building near the Director's residence in the Gardens. In 1860–1861 it moved to a building in the Domain. In 1935 the herbarium was moved to a substantial building on the present site, and a new wing was completed in 1989 (Ross, 1989). It now contains over 1 million specimens.

In December 1925 the Rev. H.M.R.Rupp donated his collection of pressed plants to the University of Melbourne. With the erection of a new building for the School of Botany (under Professor A.J.Ewart) in 1929, the collection formed the beginning of a university herbarium (now MELU). This herbarium has grown over the years, and now has more than 120 000 collections covering all major plant groups. It is used for both teaching and research, and includes important collections by Rupp (particularly orchids), Ilma Stone (mosses), G.Beaton (fungi), and G.T.Kraft, S.C.Ducker and others (algae). Curators/Keepers of the herbarium have included H.B.Williamson (1929–1931), W.H.Nicholls (1934–1951), E.McLennan (1957–1972), S.L.Duigan (c. 1955–?1989), K.Wilson (?–?) and P.Y.Ladiges (?1989–).

Smaller university herbaria are maintained at Monash University (MUCV, c. 15 000 specimens) and La Trobe University (LTB, c. 20 000 specimens).

In recent years major taxonomic contributions from Victorian botanists have included those by David Albrecht (Epacridaceae), Helen Aston (aquatic families), Geoff Carr (Orchidaceae), Margaret Clayton (Phaeophyta), Margaret Corrick (*Pultenaea*), Andrew Drinnan (Myrtaceae, Winteraceae), Sophie Ducker (marine algae, history of botany), Marco Durretto (*Boronia*), Tim Entwisle (freshwater algae, *Flora of Victoria*), Rex Filson (lichens), Stephen Forbes (Asteraceae, Poaceae), Don Foreman (Proteaceae, *Flora of Victoria*), Geoff Jeans (Orchidaceae), Gerry Kraft (marine algae), Pauline Ladiges (*Eucalyptus*), Tom May (fungi), Patrick McCarthy (lichens), Jim Ross (Caesalpiniaceae, Fabaceae, Mimosaceae), George Scott (bryophytes), Philip Short (Asteraceae), Ilma Stone (mosses), Kevin Thiele (*Banksia*), Trevor Whiffin (interactive key to rainforest taxa), Frank Udovicic (Myrtaceae), Neville Walsh (*Pomaderris*, *Flora of Victoria*), Bill Woelkerling (coralline algae). Helen Cohn has published extensively on the history of botany and botanists.

Victoria has always been well-served with Floras. The presence of Mueller, and his collaboration with Bentham, ensured that Victorian plants were well-described in *Flora Australiensis*. Ewart wrote the first comprehensive *Flora of Victoria* in 1931, which was replaced in 1962 and 1972 by a new 2-volume work *A Handbook to Plants in Victoria* by J.H.Willis. Volume 1 of a proposed 4-volume multi-author *Flora of Victoria* was published in 1993, Volume 2 in 1994 and Volume 3 in 1996. In 1955 the Melbourne herbarium began occasional publication of taxonomic monographs in the journal *Muelleria*. In recent years this journal has become an annual publication.

References: Jessep, 1947; Hyams, 1969; Law-Smith, 1984; Willis, 1988a; Aston, 1991; Churchill, 1991; Ross, 1991a, 1991b; Willis & Cohn, 1993; Ladiges (*pers. comm.*).

Tasmania

The earliest collections made in Tasmania by voyagers (Anderson, Labillardière, Nelson) or land-based visitors and settlers (Brown, Caley, Allan Cunningham, Lawrence) were deposited in overseas herbaria (mainly BM, K and P). In 1896 Leonard Rodway was appointed Government Botanist, a position he held until 1932, when it lapsed. In 1928 an herbarium was established at the Tasmanian Museum under the honorary directorship of Rodway. This herbarium brought together the collections of Joseph Milligan, presented to the Museum in 1852, some Mueller collections presented in 1857, some Gunn and Hooker collections (including a few from the *Erebus* and *Terror* expedition) presented to the Royal Society of Tasmania in 1861, and Gunn's herbarium, presented in 1876. From 1928 until 1932 the Herbarium was housed at the Botanic Gardens, then part of the Museum. Rodway's wife, Olive Rodway, was appointed Keeper (1932–1941) and the Herbarium was moved to the Museum. During this period Rodway's private herbarium was added, along with that of R.L.G.Brett (*Eucalyptus*). From 1941 the Herbarium was moved back to the Botanic Gardens, and Winifred Curtis (lecturer in Botany at the University of Tasmania) was appointed part-time Curator until 1946.

In 1946 a separate teaching herbarium was established in the University by Curtis, H.D.Gordon and J.Somerville. In 1946 the Museum Herbarium was moved again, on long-term loan to the Botany Department, University of Tasmania. The Museum and Botanic Gardens were separated administratively in 1950, and the Herbarium became the responsibility of the Botanic Gardens, although still housed at the University. Janet Somerville was Honorary Curator 1957–1963. As the result of a Report prepared by John Parham in 1976, a formal Tasmanian Herbarium (HO) was established. The Tasmanian Herbarium amalgamated the collections of the Botanic Gardens, Museum and University under the control of the Museum, and in 1978 Tony Orchard was appointed as the first salaried Curator. He remained in this position until 1992, being succeeded by Gintaras Kantvilas (lichens). A purpose-built herbarium was constructed on the University site and occupied in 1987, although the Tasmanian Herbarium remains administratively part of the Tasmanian Museum and Art Gallery.

A second herbarium has been maintained for some years in Launceston, at the Queen Victoria Museum, under the part-time curatorship of Mary Cameron.

Historically, much of the taxonomic research on the Tasmanian flora has been carried on outside the State. Leonard Rodway was the first resident to publish extensively, with papers on the vascular flora, bryophytes and fungi. From 1939 Winifred Curtis took up the mantle, and with the assistance of Dennis Morris since 1970, has written extensively on a number of groups. Since formal establishment of the Tasmanian Herbarium in 1975, Tony Orchard (Asteraceae, Haloragaceae, *Micranthemum, Persoonia*), and Alex Buchanan (Asteraceae, Census, history of collectors) have also made contributions to the knowledge of the vascular flora, while Gintaras Kantvilas has conducted extensive research on the lichens. University staff and others associated with the Herbarium include Ron Crowden (Epacridaceae), Alan Gray (Epacridaceae, *Eucalyptus*, *Telopea*) and Yvonne Menadue (Epacridaceae, Ranunculaceae).

Tasmania has been well-served with Floras. Robert Brown's *Prodromus Florae Novae Hollandiae et Insulae van Diemen* (1802–1805) and Labillardière's *Novae Hollandiae Plantarum Specimen* (1804–1807) were heavily based on Tasmanian collections, while J.D.Hooker's *Flora Tasmaniae* (1855–1860) was the most comprehensive account of Australian plants written to that time. The first locally-produced Flora was *Handbook of the Plants of Tasmania* (Spicer, 1878). Rodway published his *The Tasmanian Flora* in 1903, and Winifred Curtis (with Dennis Morris) published *The Student's Flora of Tasmania* (describing the flowering plants and gymnosperms) in 4 volumes (5 parts) between 1956 and 1994. Curtis and Margaret Stones prepared the lavishly illustrated *The Endemic Flora of Tasmania* in six volumes (1967–1978). From 1969 to 1991 Tasmanian grasses were studied using Jocelyn Townrow's *A species list of and keys to the grasses of Tasmania* (*Pap. & Proc. Roy. Soc. Tasmania* 103: 69–96, 1969). A *Census of the Vascular Plants of Tasmania* was published in 1995 by Alex Buchanan. The Tasmanian Herbarium has since 1988 produced a series of monographs under the title *Occasional Publications of the Tasmanian Herbarium*.

References: Gordon, 1947; Orchard, 1987; John Parham (*pers. comm.*).

Botanists, collectors, early voyagers and other describers of Australian plants

Alcock, C. Ray

Born in Mount Gambier, South Australia, on 12 December 1921.

Employed for most of his life as a weeds officer in the Department of Agriculture, based mainly on Eyre Peninsula, South Australia, he assembled a personal herbarium of over 10 000 specimens, which are lodged at AD, with duplicates in a number of other institutions.

Reference: Hall, 1993.

Allen, Charles E.F.

Born in Devonshire, England, on 2 July 1876, died some time after 1939.

Curator, Darwin Botanic Gardens, 1913–1935. His main interest was in economic plants, but he collected widely and sent material for identification to various herbaria. Specimens collected by him are in K, MEL and NSW.

References: Hall, 1978; Bauer, 1980.

Anderson, James

Born in Boguham, Scotland, in 1797, died in Sydney, New South Wales, on 22 April 1842.

Before arriving in Sydney in 1832, Anderson had collected in Sierra Leone, Ascension Island, Brazil and Chile. He was botanical collector on King's voyages (1818–1821). Succeeded Allan Cunningham as New South Wales Colonial Botanist and Superintendent of the Botanic Gardens from 1838. His collections were sent to K, with others now in CGE, G, GOET, MO, NSW and OXF.

References: Bailey, 1891; Maiden, 1908a; Froggatt, 1932; Osborn, 1952; Olde & Marriott, 1994.

Anderson, Robert H.

Born in Cooma, New South Wales, on 12 March 1899, died in Chatsworth, New South Wales, on 17 August 1969.

Appointed to the National Herbarium of New South Wales in 1921 as Assistant Botanist, becoming Botanist and Curator in 1936. This position was renamed Chief Botanist (1936), was reunited with that of Superintendent of the Gardens (1945), and was later (1960) designated Director, Royal Botanic Gardens and National Herbarium. Under his direction the journal *Contributions from the New South Wales National Herbarium*, and its companion *Flora* series were initiated. His taxonomic research was mainly in the family Chenopodiaceae, and his herbarium is to be found at NSW, with some duplicates in A, MEL and MO.

Reference: Vickery, 1972.

Anderson, William

Born in North Berwick, England, on 28 December 1750, died off the coast of Russian Asia on 3 August 1778.

On board the *Resolution* on Cook's second voyage, but this ship did not visit Australia. Surgeon and naturalist on the *Resolution*, on Cook's third voyage (1776–1780). Collected at Adventure Bay, Bruny Island, Tasmania (26–30 January 1777). His collection is at BM, with some duplicates at WELT.

References: Bailey, 1891; Maiden, 1909a, 1921; Finney, 1984.

Andrews, Cecil R.P.

Born in London, England, on 2 February 1870, died in England on 13 June 1951.

Principal of the (Teachers) Training College, Claremont, Western Australia (1901–1903); Director of Education for Western Australia (1903–1929); Pro-Chancellor of the University of Western Australia (1912–1929); returned to England in 1929–1930. Published a number of papers on various groups, including *Acacia*, *Eriostemon*, *Eucalyptus* and *Pultenaea*. His collections are in PERTH, and include a number from the Perth region from areas now covered in suburbs.

References: Hall, 1978, 1989; Olde & Marriott, 1994.

Archer, William H.

Born in Launceston, Tasmania, on 16 May 1820, died at Fairfield near Longford, Tasmania, on 14 October 1874.

A wealthy landowner and architect, later a parliamentarian, who owned a property 'Cheshunt' near Deloraine, Tasmania. Collected in the 1840s and 1850s in the vicinity of his property. Some of his specimens were incorporated into Gunn's herbarium, but the majority were taken by him to K when he travelled to England to assist J.D.Hooker with *Flora Tasmaniae* (1859) both monetarily and as a botanical artist. A few duplicates can be found in C, FI, GH, HO, L, MANCH, MO, NSW and W.

References: Maiden, 1909; Hall, 1978; Buchanan, 1988b, 1990; Conn, 1994.

Armit, William E.de M.

Born in Liège, Belgium, in 1848, died in (?) Ioma, New Guinea, on 3 January 1901.

An officer of the Queensland Mounted Police who collected in northern Queensland (e.g. Gilbert, Lynd, Herbert and Burdekin Rivers) for F.Mueller. He left Queensland about 1882 and became an official (Sub-collector of Customs, Resident Magistrate) in New Guinea. His Queensland collections are in MEL.

References: Maiden, 1910a, 1921; Hall, 1984.

Armstrong, John W.

Date of birth unknown, died in Koepang, Timor, on 21 January 1847.

Came to Australia from Belize, British Honduras. From about 1838 connected with the Government Gardens at Port Essington, collecting for Kew, and travelling to Timor at least twice. His Australian collections date from 1838 until at least August 1846, those from Timor from 1840 to 1845. His main collection is in K, with duplicates in BM and CU.

References: Bailey, 1891; Maiden, 1908c; Hall, 1984; Bean, 1996.

Aston, Helen I.

Born 1934.

In a career spanning 34 years (1956–1991) at the National Herbarium of Victoria, Helen Aston became one of Australia's leading authorities on freshwater vascular plants. In particular, she has published revisional work on Juncaginaceae, Menyanthaceae (*Nymphoides*, *Villarsia*) and Pontederiaceae. She is perhaps best known for her pioneering book *Aquatic Plants of Australia* (1977), but has also made major contributions to the *Flora of Australia* (Podostemaceae, Pontederiaceae and Sparganiaceae) and in retirement has three more family treatments in preparation (Juncaginaceae, Limnocharitaceae and Menyanthaceae). She also has a strong interest in ornithology. Her main herbarium is at MEL, with duplicates in several other Australian herbaria.

Reference: Cohn, 1991.

Portraits: Aston, 1973 (dustjacket); Cohn, 1991.

Atkinson, C. Louisa W.

Born in Oldbury, Sutton Forest, New South Wales, on 25 February 1834, died in Swanton, near Oldbury, New South Wales, on 28 April 1872.

Australia's first native-born woman novelist, as well as an accomplished naturalist, artist and journalist. Collected extensively around Kurrajong and Berrima, New South Wales, and a colleague of William Woolls. Many of her specimens were sent to F.Mueller, and are now to be found in MEL (some also in JE).

References: Maiden, 1912; Moyal, 1981; Gilbert, 1985; P.Clarke, 1990; Lawson, 1995.

Portraits: Hall, 1978; Gilbert, 1985; P.Clarke, 1990; Martin, 1996.

Babbage, Benjamin H.

Born in England in 1815, died in St Marys, South Australia, on 20 October 1878.

Collected north of Mt Searle and to Blanchewater, South Australia, in 1856. In 1858 he led an expedition in South Australia towards Lake Torrens, exploring the eastern shores of Lake Gairdner, Lake Macfarlane, Lake Hart and Island Lagoon. The botanist on the latter expedition was J.F.A.D.Herrgott. Specimens from both expeditions are in K and MEL.

References: Maiden, 1908c; Hall, 1984; Kraehenbuehl, 1986; Olde & Marriott, 1994.

Portrait: Kraehenbuehl, 1986.

Backhouse, James

Born in Darlington, Yorkshire, England, on 8 July 1794, died in York, England, on 20 January 1869.

Nurseryman and Quaker missionary, who from 1832–1838 collected in all the Australian colonies, and on Norfolk Island, later visiting Mauritius and South Africa (1838–1841). In Tasmania 1832–1834. He wrote on botany, the Aborigines and sociological problems, among other things, and his botanical work was held in high regard by J.D.Hooker. His main collection is now at K, with a few duplicates at DBN, HO, MEL and MO.

References: Bailey, 1891; Maiden, 1908a, 1908c, 1909a, 1909b, 1910a; J.Willis, 1949a; Gilbert, 1952; Hall, 1978; Nelson, 1980; Kraehenbuehl, 1986; Buchanan, 1988b, 1990; Barker & Barker, 1990; Symons & Symons, 1997b.

Portrait: Gilbert, 1981.

Baeuerlen, William (Wilhelm Bäuerlen)

Born in Neidernhall, Germany, on 27 October 1840, died in Sydney, New South Wales, on 28 October 1917.

Left Germany in 1863, and by 1883 was collecting specimens in Australia for F.Mueller. From about September 1883 until April 1905 Baeuerlen collected extensively in New South Wales (particularly in the north-east, around Lismore and Ballina in the 'Big Scrub', but also in the north-west, central, south-east and central coast areas), in south-eastern Queensland and in east Gippsland, Victoria. From 1883 until at least 1888 he was contracted as a collector for F.Mueller (MEL), and from 1886 for J.H.Maiden (NSW). In 1886 he was appointed botanical collector of the *Bonito* expedition which spent four months in the Fly and Strickland Rivers in Papua New Guinea His collections amount to many thousands of specimens, of which about 70 serve as Types for new species and infraspecific taxa. The main holdings are at MEL and NSW, with a few in A, B, KIEL, M and P.

References: Hall, 1978; Wilson, 1990; Hall, 1992; Olde & Marriott, 1994.

Portrait: Wilson, 1990.

Map of collecting localities: Wilson, 1990.

Bailey, Frederick M.

Born in Hackney, England, on 25 March 1827, died in Brisbane, Queensland, on 25 June 1915.

Father of John Bailey (Government Botanist of South Australia, and first curator of the Adelaide Botanic Gardens). Settled in Brisbane, in 1861, setting up a seedsman's business, and selling plant collections to British and European herbaria. He was appointed in 1875 to a Government Board set up to investigate diseases of livestock and plants, and travelled extensively throughout Queensland in search of poisonous plants. He became Acting Curator of the Queensland Museum in 1880–1881, and was appointed Queensland Colonial Botanist in 1881, a position he held until his death. He conducted numerous collecting expeditions, the most important being to Rockingham Bay, Seaview Range and the upper Herbert River (1873), western Queensland, Roma and Rockhampton (1876), Cairns and the Barron River (1877), Bellenden Ker (1889), Georgina River (1895), Torres Strait (1897) and British New Guinea (1898). He published many papers on the Queensland flora, and several books, including *Handbook of the Ferns of Queensland* (1874), *Illustrated Monograph of the Grasses of Queensland* (1878) and the 7-volume *The Queensland Flora* (1899–1902, 1905). The latter is still the only State-wide Flora to have been produced, and was compiled by extracting Queensland-related material from Bentham's *Flora Australiensis*, and supplementing this with information from Mueller's two Censuses, and Bailey's own local knowledge. A full bibliography of Bailey's work is given by Johnston (1916). Over 50 species have been named in his honour. The majority of his specimens are in BRI, with some Types at BM. Small quantities of material are also at A, AK, B, BM, CGE, DS, H, HO, K, L, M, MANCH, MEL, MO, NSW, OXF, P, PC, US.

References: Bailey, 1891; Johnston, 1916; Maiden, 1921; White, 1949; Hall, 1978; Everist, 1982; Henderson, 1984; Olde & Marriott, 1994.

Partial itineraries and bibliographies: Bailey, 1891; White, 1949.

Bailey, John F.

Born in Brisbane, Queensland, on 5 August 1866, died in Brisbane on 19 May 1938.

Son of F.M.Bailey, and worked as his assistant from 1889, before being appointed Curator of the Brisbane Botanic Gardens (1905–1916). He succeeded his father as Government Botanist for 18 months in 1915–1916 before moving to Adelaide as Director of that Botanic Garden (1917–1932). His herbarium is in A, BRI and K.

References: Everist, 1982; Olde & Marriott, 1994.

Baker, Richard T.

Born in Woolwich, England, on 1 December 1855, died in Sydney, New South Wales, on 14 July 1941.

Arrived in Australia in 1879, and succeeded Maiden as Curator and Economic Botanist at the Sydney Technological Museum in 1901, retiring in 1921. Best remembered for his work on the economic values of pines and *Eucalyptus*, especially their timbers and essential oils. His herbarium is in NSW and NSWF, with a few duplicates in A, BM, DBN, K and MEL.

References: Walkom, 1942; Hall, 1978; Nelson, 1980; Olde & Marriott, 1994.

Bancroft, Joseph

Born in Streatford, England, on 21 February 1836, died in Brisbane, Queensland, on 16 June 1894.

Specialised mainly in the study of plants of economic importance, especially those of pharmacological value (e.g. *Duboisia*), and plant diseases. In some of these studies he was followed by his son, Thomas L. Bancroft (1860–1933). His collections are at K.

References: Maiden, 1910a; Hall, 1978, 1984.

Portrait: Maiden, 1910a.

Banks, Joseph

Born in London, England, on 13 February 1743, died near London on 19 June 1820.

A gentleman of independent means, and patron of many scientific endeavours connected with Australia. Accompanied Cook on his first voyage to Australia (1770), collecting extensively (with Solander) at Botany Bay, Bustard Bay and Cape Grafton (New South Wales) and Endeavour River, Point Hillock, Thirsty Sound, Lizard Island and Booby Island (Queensland). A close friend of King George III, and through him given the job of special advisor and director of the Royal Gardens at Kew (1773–1820). Subsequently Banks arranged for a series of collectors to travel the world in search of seeds and plants for Kew. In the Australian context these included R.Brown, J.Burton, G.Caley, A.Cunningham, R.Cunningham and A.Menzies. He was President of the Royal Society from 1778 until his death, and maintained a large library and herbarium at Soho Square which was freely accessible to visiting botanists. His botanists/librarians were successively Solander, Dryander and Brown. Banks published very little himself, but his patronage was invaluable in the natural history world of his time. Many aspects of his life were recently reviewed in a major symposium (Banks *et al.*, 1994). His collections of about 23 400 specimens are housed at BM with small numbers of duplicates in AK, B, BRI, C, CAL, CANB, E, HAL, HO, LINN, LIV, MEL, MO, NSW (c. 760 Banks & Solander collections), P, P-JU, PERTH, S, US, W, WELT.

References: Bailey, 1891; Maiden, 1908a; Lyte, 1980; Gilbert, 1981; Finney, 1984; Carter, 1987, 1988; O'Brian, 1988; Gascoigne, 1994; Olde & Marriott, 1994; Banks *et al.*, 1994; Hansen & Wagner, 1998.

Portraits: Lyte, 1980; Gilbert, 1981; O'Brian, 1988; Gascoigne, 1994; Olde & Marriott, 1994; Duyker & Tingbrand, 1995.

Basedow, Herbert

Born in Kent Town, South Australia, on 27 October 1881, died in the same town on 4 June 1933.

Probably best remembered as an anthropologist, geologist and medical practitioner, he led an expedition in 1926 into northern and north-western South Australia which reached as far north as Uluṟu [Ayers Rock] in the Northern Territory. He visited Arnhem Land, Northern Territory, in 1928 with D.Mackay. In 1911 briefly appointed Chief Protector of Aborigines in the Northern Territory. He wrote extensively on botany, geology and anthropology. Some collections are also known from the Kimberley region, Western Australia. He is reported to have given specimens to Diels at Marburg, but there are also collections at AD, B, K and NSW.

References: Hall, 1978; Kraehenbuehl, 1986.

Portrait: Kraehenbuehl, 1986.

Bauer, Ferdinand L.

Born in Feldsberg, Austria, on 20 June 1760, died in Heitzing, Vienna, Austria, on 17 March 1826.

He and his brother Franz were probably two of the best of all botanical artists. Engaged by Banks to join Flinders' expedition to Australia 1801–1803 as botanical draughtsman, Bauer also made a large number of collections, including some from Norfolk Island, which was not visited by Brown. Some of these collections may have been attributed to Robert Brown subsequently, but many with Bauer as collector are to be found in W, with duplicates in B, HBG, K. Bauer remained in Australia until 1805.

References: Maiden, 1921; Edwards, 1976; Hall, 1978; Gilbert, 1981; Edwards, 1981b; Finney, 1984; Clarkson, 1988 (incl. footnote by M.D.Crisp); Olde & Marriott, 1994; Lack, 1997.

Baxter, William

Date of birth unknown, died about 1836.

An English gardener who visited Australia collecting seeds and plants for British nurserymen. Collected on Kangaroo Island, South Australia (1822–1823), and possibly again in South Australia along the south coast in 1829. Later he collected along the southern coast of Western Australia (1823–1825, 1828–1829) at King George Sound, Cape Arid and Lucky Bay for nurserymen and private individuals. He also collected at Twofold Bay, New South Wales, and at Wilsons Promontory, Victoria (1826). His last expedition in 1828–1829 to Western Australia was arranged by Charles Fraser, in part to collect material for the Sydney Botanic Gardens, New South Wales, but the two disagreed over division of the material on his return. His collections are housed at BM and K, with a few duplicates at CGE, DBN, FI, MO and NY.

References: Bailey, 1891; Maiden, 1908c, 1909b; Hall, 1978; Nelson, 1980; Finney, 1984; Kraehenbuehl, 1986; Barker & Barker, 1990; Olde & Marriott, 1994.

Beadle, Noel C.W.

Born 1914, died at Guyra, New South Wales, on 13 October 1998.

Trained at the University of Sydney, subsequently working for the New South Wales Soil Conservation Service, and as a lecturer in botany at the University of Sydney. He was foundation Professor of Botany at the University of New England, Armidale, from 1954 until retirement, and remained Emeritus Professor at that university until his death. He wrote the Student's Flora of North-eastern New South Wales (6 parts, 1971–1987), and was co-author of Handbook of the Vascular Plants of the Sydney District and Blue Mountains (1963) and its successor Flora of the Sydney Region (first 3 edns & reprints, 1972–1991). His herbarium is housed in NE.

References: Dustjacket, *Flora of the Sydney Region* edn 3, 1986; Olde & Marriott, 1994; Beadle, 1995.

Portraits: Beadle, 1995.

Beard, John S.

Born in Gerrards Cross, England, on 15 February 1916.

Came to Australia in 1961 after some years in the West Indies and Natal. Director of King's Park and Botanic Garden, Perth, Western Australia (1961–1970) and Director, Royal Botanic Gardens & National Herbarium, Sydney, New South Wales (1970–1972). Perhaps best known in Australia for his work on vegetation and vegetation mapping, especially *Vegetation Survey of Western Australia* (1974–1981).

References: Hall, 1979; Olde & Marriott, 1994.

Beauglehole, A. Clifford

Born 1920.

An orchardist at Portland, Victoria, who throughout his life has taken an intense interest in the plants of Victoria, and to a lesser extent, the rest of the country. His herbarium in 1993 was estimated at over 90 000 specimens. Many of these were vouchers for an ambitious project to survey each of Victoria's Study Areas (established by the Land Conservation Council) for distribution and conservation of vascular plants. His main herbarium is being progressively lodged in MEL, with numerous duplicates elsewhere (e.g. AD, PERTH).

References: Kraehenbuehl, 1983b, 1983c; Willis & Cohn, 1993; Olde & Marriott, 1994.

Portrait: Kraehenbuehl, 1983c.

Beckler, Hermann

Born in Germany in 1828, died in 1914.

Beckler's early collections were made in south-eastern Queensland and on the north coast of New South Wales. In 1860–1861 he was medical officer and botanist on the Burke and Wills Victoria Exploring Expedition, collecting in the Scrope Range and other parts of western New South Wales. Accompanied the Neumayer magnetic survey of north-western Victoria, September–November 1861. Later employed by Mueller as a collector, particularly in northern New South Wales on the Hastings, Richmond, Macleay and Clarence Rivers, and at Moreton Bay, Queensland. His main collections are in MEL, with some in M.

References: Bailey, 1891; Willis, 1962; Hall, 1978; Cohn & Almond, 1991; Willis & Cohn, 1993.

List of collecting localities: Willis, 1962.

Behr, Hans H.

Born in Keothen, Germany, on 18 August 1818, died in San Francisco, U.S.A., on 6 March 1904.

Trained as a physician, Behr had a strong interest in most aspects of natural history. He arrived at Port Adelaide, South Australia, on 12 September 1844, and spent the next 13 months collecting in the Barossa Valley, on the plains south of Adelaide, and along the lower Murray River and in the Murray Scrub. He returned to Germany in 1847 before visiting South Australia again from 6 November 1848 to late-1849, collecting in similar localities. After leaving Australia he settled briefly in the Philippines, before moving to San

Francisco, where he became a member of the California Academy of Sciences, and Professor of Botany at the California College of Pharmacy. His discoveries were published, in the main, by Schlechtendal, but he also corresponded regularly with Ferdinand Mueller. His main herbarium is now housed in HAL, but a considerable number of specimens are also in MEL, probably purchased with the Sonder herbarium. His later collections are in CAS.

References: Maiden, 1908c, 1912; Hall, 1978; Kraehenbuehl, 1981a, 1986; Olde & Marriott, 1994.

Portraits: Kraehenbuehl, 1981a, 1986.

Itineraries: Kraehenbuehl, 1981a.

Bennett, John J.

Born in Tottenham, England, on 8 January 1801, died in Maresfield, Sussex, England, on 29 February 1876.

Secretary of the Linnean Society (London) from 1840–1860. Worked in the Botany Department, British Museum from 1827, Keeper of Botany from 1857–1870. He was Assistant to Robert Brown and legatee of his herbarium. It is usually stated that Bennett added numbers to Brown's Iter Australiense specimens, numbers which have often been mistaken for collector numbers (sometimes cited as 'Bennett numbers' in *Flora of Australia*), although Edwards (1976) suggests these numbers were added by James Britten (1846–1924) and Henry Trimen (1843–1896). Bennett described a few Australian species.

References: Carruthers, 1876; Maiden, 1908a; Edwards, 1976.

Portrait: Mabberley, 1985.

Bentham, George

Born in Stoke, Plymouth, England, on 22 September 1800, died in London, England, on 10 September 1884.

Patron of botany, of independent means, Bentham never visited Australia himself. President of the Linnean Society (1861–1874). Author of many important works, including *Flora Hongkongensis* (1861), *Genera Plantarum* (1862–1883, with J.D.Hooker) and *Flora Australiensis* (1863–1878). The latter was written mainly from specimens held in Europe. These included the Hooker herbarium at K, the Brown and the Banks & Solander herbaria at BM, Lindley's herbarium (now CGE), and Sonder's herbarium from Hamburg. He visited Paris to examine French collections, particularly those of Labillardière, and saw Hügel's collections at Vienna. The contents of the Melbourne Herbarium (MEL) were loaned sequentially to him over 16 years by its curator, Ferdinand Mueller. The MEL specimens seen by Bentham were subsequently initialled 'B' on a turned over corner of their label, on their return (Ross, 1995). In the Preface to the *Flora Australiensis* Bentham provides brief notes on many of the collectors mentioned in his work.

References: Maiden, 1908a, 1909b; Daley, 1927; Blake, 1954; Hall, 1978; Henderson, 1978; Olde & Marriott, 1994; Ross, 1995; Filipiuk, 1997.

Portraits: Hall, 1978; Gilbert, 1981; Olde & Marriott, 1994; Filipiuk, 1997.

Betche, D. Ernst L.

Born in Potsdam, Germany, on 31 December 1851, died in Sydney, New South Wales, on 28 June 1913.

Trained as a horticulturalist in Germany, Betche arrived in Sydney in 1881 and almost immediately was appointed collector for the Sydney Botanic Gardens, New South Wales. Promoted to Botanic Assistant (to Maiden) from 1897. With C.Moore he wrote *The Handbook of the Flora of New South Wales* (1893) and with J.H.Maiden, *Census of New South Wales Plants* (1916), published after his death. He cooperated with Maiden on various short notes on the flora of New South Wales, and himself published on Goodeniaceae. His herbarium is to be found in NSW.

References: Maiden, 1921; Froggatt, 1932; Cheel, 1947; Hall, 1978; Vallance, 1983; Olde & Marriott, 1994.

Portrait: Maiden, 1921.

Bidwill, John C.

Born in St Thomas's, England, in February 1815, died in Tinana, Wide Bay, Queensland, on 16 March 1853.

First arrived in Sydney, New South Wales, in September 1838. Visited New Zealand (Bay of Plenty and central North Island) from 5 February until April 1839, and again in 1840, and Moreton Bay, Queensland, in 1841, before returning to England in 1843. He returned to Sydney in 1844, travelling from there to New Zealand in the same year and Tahiti in 1845. First Director of Botanic Gardens, Sydney, and Government Botanist, 1 September 1847–January 1848. Commissioner of Crown Lands, Wide Bay, Queensland (then N.S.W.) from 1848. Collected extensively, and published the first account of the Bunya Pine (*Araucaria bidwillii*). He sent many living plants and seeds to various gardens in England, including Kew, and advised William Macarthur, among others, on the introduction of plants to the colony of New South Wales. He was also an accomplished plant hybridiser. His herbarium is lodged at K, with other material in B, L, MEL and MO. Biographical materials assembled by V.Crew are in BRI.

Reference: Maiden, 1908a, 1910a; Froggatt, 1932; Hall, 1978; Henderson, 1990; Mabberley, 1996.

Black, John McC.

Born in Wigtown, Scotland, on 28 April 1855, died in Adelaide, South Australia, on 2 December 1951.

Arrived in Adelaide 1877, farming for five years before joining the literary staff of Adelaide daily newspapers and Hansard. Retired in 1902, Black undertook studies of the South Australian flora, describing some seven genera, 180 species and 40 varieties. In 1909 he published the first book on naturalised plants in Australia *The Naturalised Flora of South Australia*. At the age of 65 he began the task of writing a *Flora of South Australia*, completing the 4-volume first edition between 1922 and 1929, and the first three parts of a second edition (1943–1952). The second edition was completed by Enid Robertson after his death. He assembled a large personal herbarium, from his own efforts and those of a network of contributors, and wrote 45 papers in addition to his books. Black's memoirs were published in 1971, and his diaries in 1986 and 1991, and three major biographical sketches are available, by Enid Robertson (1978), and by Con Eardley and Marjorie Andrew (both in Barker, 1992). His herbarium was bequeathed to the University of Adelaide (ADU) and was transferred on permanent loan to AD in 1954.

References: Eardley, 1952; Black, 1971; Hall, 1978; Robertson, 1978; Kraehenbuehl, 1983c; Andrew & Clissold, 1986, 1991; Kraehenbuehl, 1986; Barker, 1992; Olde & Marriott, 1994.

Portraits: Jessop & Toelken, 1986; Barker, 1992.

Itineraries: Andrew & Clissold, 1986, 1991; Andrew *in* Barker, 1992.

Black, Raleigh A.

Born on 11 March 1880, probably at Aberdeen, Scotland, died in Mont Albert, Victoria, on 2 July 1963.

Resident in Tasmania from 1890–1926, thereafter in Victoria and (briefly) in Sydney, New South Wales. Black worked at first in a printing works, spent 26 years with the Tasmanian

Council of Agriculture, and finally, worked as a travelling representative for a fertiliser company in country Victoria. He was a close associate of Leonard Rodway. His collection of about 15 000 specimens (including around 6000 duplicates) was offered for sale to several herbaria, and was eventually purchased by MEL in August 1957. A few duplicates are also in HO, K and US.

References: Willis, 1967; Hall, 1978; Short, 1990b; Willis & Cohn, 1993.

Portrait: Willis, 1967.

Blackall, William E.

Born in Folkestone, Kent, England, in 1876, died in Perth, Western Australia, in 1941.

A medical practitioner who took a keen interest in the flora of Western Australia, beginning production of an illustrated key from about the 1920s. This work, *How to Know Western Australian Wildflowers*, was completed after Blackall's death by Professor B.J.Grieve, and remains one of the most useful guides to the Western Australian flora, particularly for the south-western flora. His herbarium of about 5000 specimens was deposited at the Western Australian Museum, and is now to be found in PERTH.

References: Grieve, 1980, 1984; Hall, 1984; Olde & Marriott, 1994.

Portrait: Grieve, 1984.

Blake, Stanley T.

Born in Brisbane, Queensland, on 3 September 1911, and died there on 24 February 1973.

Botanist to the CSIRO Northern Australia Regional Survey (1946–1947); botanist and senior botanist at the Queensland Herbarium 1946–1973. Specialised in taxonomy of tropical and subtropical grasses, Cyperaceae, *Eucalyptus*, Idiospermaceae, *Melaleuca* and *Plectranthus*. His main collection is at BRI, with some duplicates at A, B, CANB, DNA, K, MEL and NSW.

References: Hall, 1978; Olde & Marriott, 1994.

Blakely, William F.

Born in Tenterfield, New South Wales, in November 1875, died at Hornsby, New South Wales, on 1 September 1941.

Joined the staff of the Sydney Botanic Gardens, New South Wales, as a gardener in 1900. From 1913–1940 he worked in the herbarium, and assisted Maiden in his revision of *Eucalyptus*, until the latter's death in 1925. In 1934 he published privately *A Key to the Eucalypts*, of which posthumous new editions were published in 1955 and 1965. He also published on Loranthaceae, *Acacia* and weeds. His herbarium is at NSW, with some duplicates at A, CORD, DBN, L, MEL and MO.

References: Anderson, 1941; Walkom, 1942; Hall, 1978; Nelson, 1980; Olde & Marriott, 1994.

Portrait: Hall, 1978.

Bleeser, Florenz A.K.

Born in Woodside, South Australia, on 5 July 1871, died in Adelaide, South Australia, on 1 November 1942.

Employed by the Postmaster-General's Department, at first in South Australia, and then from 1889 to 1942 at Darwin, Northern Territory, where he was Assistant Postmaster. Collected widely in the Top End, sending specimens to B, K, MEL and NSW. A large part of his collection was destroyed by looters during his wartime evacuation from Darwin in February 1942. The specimens in B were lost through wartime bombing.

References: McKee, 1963; Willis, 1966; Hall, 1978; Olde & Marriott, 1994.

Boomsma, Clifford D.

Born in South Australia on 20 October 1915.

A forester with the Woods and Forests Department of South Australia who has developed a wide knowledge of the trees of that State, particularly *Eucalyptus* and *Acacia*. His major publication is *Native Trees of South Australia* (1972), but he has written a number of other departmental and scientific papers. His collections are housed at AD.

Reference: Hall, 1978.

Boorman, John L.

Born in England in 1864 or 1865, died in Liverpool, New South Wales, on 18 November 1938.

Trained at Kew, Boorman joined the staff of the Sydney Botanic Gardens, New South Wales, in January 1887. He was officially collector for the herbarium from 1901 until retirement (about 1930), accompanying Maiden on several trips, including one to Norfolk Island in 1902. Subsequently undertook extensive collecting throughout New South Wales. His main herbarium is at NSW, with some duplicates at A, BR, DBN, F, GB, GH, JE, L, MEL, MIN, MO, NY, P, S, UC, US, VT and WAG.

References: Hall, 1978; Nelson, 1980.

Bowman, Edward M.

Born in Sydney, New South Wales, in 1826, died in Clermont, Queensland, on 30 June 1872.

A nephew of William Macarthur, Bowman collected widely in central-eastern Queensland in the 1860s and 1870s, sending his specimens to F.Mueller. Many of his collecting localities are obscure or ambiguous; many were resolved by Blake (1954). Bowman's collections are now in MEL.

References: Maiden, 1910a; Blake, 1954; Hall, 1978.

Map of collecting localities: Blake, 1954.

Brass, Leonard J.

Born in Toowoomba, Queensland, on 17 May 1900, died in Cairns, Queensland, on 29 August 1971.

Trained at the Queensland Herbarium, Brass spent most of his botanical life collecting in New Guinea, most notably as a member of the Archbold expeditions from 1925. He also collected on Cape York Peninsula, Solomon Islands and in tropical Africa. His Australian collections can be found in A, B, BRI, CANB, K, NY and US. His extra-Australian collections are widely distributed in more than 20 herbaria.

References: L.Perry, 1971; Hall, 1978.

Portrait: L.Perry, 1971.

Brett, Robert L.G.

Born in Launceston, Tasmania, on 27 November 1898, died in Hobart, Tasmania, on 9 March 1975.

A school teacher in mathematics and physics, who retired as Senior Superintendent of High Schools in Tasmania. Brett took an intense interest in the eucalypts of Tasmania, collecting extensively and making notes on variation and hybridisation. His herbarium was purchased by the Tasmanian Biological Survey in 1938 and deposited in the Museum collection. Brett subsequently assembled another collection, most (?all) of which was destroyed in a bushfire in 1967. His original collection is now in HO.

Reference: Hall, 1978.

Brooks, Sarah T.

Born on board ship, Plymouth, England, on 19 September 1850, died in Norseman, Western Australia, on 23 September 1928.

Arrived with her family in Victoria in 1851, and moved to Western Australia in 1873. In 1883 she was recruited by Mueller as a collector, and collected for him until his death in 1896. Her collections are from the Israelite Bay–Mt Ragged–Pine Hill district Western Australia, and can be found in MEL.

References: Hammersley, 1981; Archer & Maroske, 1996.

Portrait: Archer & Maroske, 1996.

Brown, John E.

Born in Scotland in 1848, died in Cottesloe, Western Australia, on 26 October 1899.

Conservator of Forests in South Australia (1879–1890); Director General of Forests of New South Wales (1890–1892); and Conservator of Forests in Western Australia (1895–1899). Best known for two books, *A Practical Treatise on Tree Culture in South Australia* (1881) and *The Forest Flora of South Australia* (1883–1890). His herbarium is in AD and MEL.

References: Maiden, 1908c; Hall, 1978.

Brown, Maitland

Born in England in July 1843, died 1905.

After emigrating to Australia he became Resident Magistrate at Geraldton, Western Australia. He accompanied F.T.Gregory's expedition to north-western Australia in 1861, sending botanical collections to F.Mueller. These are now in MEL.

References: Hall, 1984; Roberts & Whitten, n.d.

Brown, Robert

Born in Montrose, Scotland, on 21 December 1773, died at Soho Square, London, England, 10 June 1858.

Studied medicine, and joined the army as a surgeon in 1795. At the invitation of Banks he was given the position of naturalist on the *Investigator*, under the command of Matthew Flinders, who carried out a circumnavigational investigation of the Australian coastline from December 1801 until June 1803. Other scientific staff on the voyage were Ferdinand Bauer (botanic draughtsman), William Westall (landscape and figure painter), John Allen (miner) and Peter Good (gardener). The voyage yielded about 3400 species. Many of the collections were subsequently lost in the wreck of the *Porpoise*. Brown stayed in Australia until May 1805, collecting on the New South Wales central coast, the islands of Bass Strait, and for 10 months in Tasmania. He succeeded Dryander as Banks' librarian, and on Banks' death in 1820 inherited his library and herbarium. This was transferred to BM, where Brown became the first Keeper of the Botanical Department. His major work on the Australian flora was his *Prodromus Florae Novae Hollandiae* (1810), but he published much else as well, including the Botanical Appendix to Charles Sturt's account of his 1844–1846 expedition to central Australia (1849). Microfilming of his diary and various other notes in the British Museum was arranged by Mary Tindale in 1952, and copies of this film are in AD, BRI, CANB, MEL, NSW and PERTH. His main herbarium (3900 specimens) is now in BM, with other major sets in E, K, LE (2055 specimens) and P (c. 1000 specimens). About 1000 specimens are in DBN, and a similar number in CANB. Some duplicates are also held in other Australian herbaria with a substantial number in MEL, and fewer in BRI, HO and NSW. Others are in AK, B, BR, C, CW, DBN, F, FI, G-DC, LINN, LIV, M, MO, NY, P-JU, S, SBT, W and WELT.

References: Bailey, 1891; Maiden, 1908c, 1909b; Burbidge, 1952; Blake, 1954; Burbidge, 1956; Willis, 1956; Willis & Skewes, 1956; Stearn, 1960; Mack, 1966; Powell & Morley, 1976; Edwards, 1976; Stearn, 1977; Hall, 1978; Nelson, 1980, 1981a; Gilbert, 1981;

Edwards, 1981b; Finney, 1984; Mabberley, 1985; Kraehenbuehl, 1986; Clarkson, 1988; Grandison, 1990a; Vallance, 1990; Cohn & Almond, 1991; Edmondson, 1993; Olde & Marriott, 1994; Maslin & Cowan, 1995; Nelson, 1996.

Portraits: J.Willis, 1949a; Hall, 1978; Gilbert, 1981; Edwards, 1981b; Mabberley, 1985; Kraehenbuehl, 1986; Vallance, 1990; Olde & Marriott, 1994.

Lists of collecting localities: Maiden, 1908c (South Australia only); Burbidge, 1956; Vallance, 1990.

Maps of voyages: Blake, 1954 (Queensland only); Mabberley, 1985; Cohn & Almond, 1991.

Burbidge, Nancy T.

Born in Cleckheaton, Yorkshire, England, on 5 August 1912, died in Canberra, Australian Capital Territory, on 4 March 1977.

Moved with her family at an early age to Western Australia. After studying botany at the University of Western Australia, she spent 18 months at Kew (1939–1940) before returning to Western Australia to work with the Institute of Agriculture and Western Australian Forestry Department. Appointed Assistant Agronomist at the Waite Institute (1943–1946) before taking up the position of Systematic Botanist at CSIRO, Division of Plant Industry, Australian Capital Territory (1946–1977). In this last position she was responsible for laying the foundations of Herbarium Australiense, later the Australian National Herbarium (CANB). From 1973–1977 she was seconded to the Australian Academy of Science as Director, *Flora of Australia* Project, although still remaining on the herbarium staff. She was an extremely strong advocate of the establishment of the Australian Biological Resources Study, and the *Flora of Australia* project in particular. Burbidge was author of two major bibliographic works, *Dictionary of Australian Plant Genera* (1963) and *Plant Taxonomic Literature in Australian Libraries* (1978), co-author (with Max Gray) of a local Flora, (*Flora of the Australian Capital Territory* 1970), a 2-volume work on grasses, *Australian Grasses* Vol. 1 (1966) and Vol. 2 (1968) as well as about 50 papers on phytogeography, ecology, botanical history, and taxonomy of Asteraceae (*Camptacra, Helichrysum, Ixodia, Vittadinia*), Fabaceae (*Sesbania*), Myrtaceae (*Eucalyptus, Thryptomene*), Poaceae (*Enneapogon, Triodia*) and Solanaceae (*Nicotiana*). As Australian Botanical Liaison Officer in Kew in 1955 she undertook the microfilming of Robert Brown's Australian notebooks. Copies of this film are in several Australian herbaria, including AD and CANB. Her early collections are in ADW (now AD) and PERTH, later ones in CANB, with duplicates in some other Australian herbaria, including MEL.

References: Hall, 1978; Hartley, 1978; Grieve, 1984.

Portrait: Hartley, 1978.

Burton, David

Born in England c. 1760s, died on the Nepean River, New South Wales, on 13 April 1792.

Sent to New South Wales in 1791 by Banks, who received collections of seeds and tubs of plants from him. He was Public Gardener and Superintendent of Convicts at Parramatta 1791–1792. His collections are in BM.

References: Bailey, 1891; Hall, 1978; Finney, 1984; Olde & Marriott, 1994.

Bynoe, Benjamin

Born about 1803, died on 13 November 1865.

Surgeon on the voyage of the *Beagle* (1837–1843). Collected at Depuch Island and the Abrolhos, (and perhaps on Dampier Peninsula) in Western Australia, Victoria River in the Northern Territory, in Bass Strait, and in New South Wales. The specimens are at BM and in W.J.Hooker's herbarium at K.

Reference: Bailey, 1891; Maiden, 1909b; Hall, 1978; Kenneally *et al*., 1996.

Byrnes, Norman B.

Born in Adelaide, South Australia, on 18 December 1922.

Botanist stationed at Darwin, Northern Territory, from 1966 until 1973, before joining the Queensland Herbarium. His research has centred on Combretaceae and Myrtaceae, and his collections are to be found in BRI and DNA.

References: Hall, 1984; Olde & Marriott, 1994.

Caley, George

Born in Craven, Yorkshire, England, on 10 June 1770, died in Bayswater, England, on 23 May 1829.

Sent to Port Jackson, New South Wales, by Banks in 1800 to gather specimens for his employer and Kew Gardens. He travelled widely in the Blue Mountains, and visited Newcastle, Jervis Bay (all New South Wales), Western Port Bay (Victoria, 1801), Norfolk Island (1805) and the Hobart Town settlement (Tasmania, 1805). He collected with Robert Brown and Ferdinand Bauer in New South Wales on several occasions in 1802–1804, and it is likely that Brown and others subsequently adopted Caley names for new taxa (Webb, 1990a). He left the colony in 1810. His main collection of about 2000 specimens was lodged in the Banks herbarium, and is now in BM, with a few duplicates in Australian and other herbaria, including A, DBN, E, FI, G, GH, HO, K, LIV, MEL, MO, NSW, OXF, P, UPS and W.

References: Bailey, 1891; Maiden, 1921; Currey, 1966; Hall, 1978; Nelson, 1980; Gilbert, 1981; Barker & Barker, 1990; Webb, 1990a, 1990b; Webb & Lister, 1991a, 1991b; Edmondson, 1993; Webb, 1995; Nelson, 1996.

Partial Itineraries: Webb & Lister, 1991a; Webb, 1995.

Cambage, Richard H.

Born in Milton, New South Wales, on 7 November 1859, died in Burwood, New South Wales, on 28 November 1928.

Trained as a surveyor, and worked for the Departments of Lands and Mines. Keenly interested in botany, he collaborated with Baker, Maiden, Woolls, and others in studies of *Acacia* and *Eucalyptus*. He travelled widely throughout New South Wales as a field surveyor, collecting extensively. His collections are in SYD, with duplicates elsewhere, including A, CANB, DBN, L, NSW and S.

References: Andrews, 1934; Hall, 1978; Nelson, 1980.

Portrait: Hall, 1978.

Carolin, Roger C.

Born in London, England, on 15 October 1929.

Appointed lecturer in Botany and Curator of the John Ray Herbarium (SYD) at the University of Sydney in 1955, eventually becoming Associate Professor, before retiring in 1989. His taxonomic research has mainly centred on the Campanulales, particularly on Brunoniaceae and Goodeniaceae. He has also published revisional treatments in Geraniaceae, and worked on cytology and hybridisation in *Dianthus*. He was co-author of the *Flora of the Sydney Region* in its various editions (1972–1993), as well as serving on the Editorial Committee for the *Flora of Central of Australia* and the *Flora of Australia*. Carolin was principal author of *Flora of Australia Vol. 35. Brunoniaceae, Goodeniaceae* (1992). During his tenure at the University of Sydney a generation of students was imbued with enthusiasm for plant taxonomy, and Sydney became a focus for taxonomic studies. His collections are mainly housed at SYD.

Reference: Morrison, 1989.

Portrait: Morrison, 1989.

Carr, S.G. Maisie (nee Fawcett)

Born in Footscray, Victoria in 1912, died in Canberra, Australian Capital Territory, on 9 September 1988.

Her early research was in the ecology of the High Country of Victoria. Later, with her husband Professor D.J.Carr, she undertook comprehensive morphological and taxonomic research into *Eucalyptus*. Coinciding with the International Botanical Congress in Sydney in 1981, they edited and wrote two volumes of historical essays on Australian botany, *People and Plants in Australia*, and *Plants and Man in Australia*. They also published two books (*Eucalyptus 1*, and *Eucalyptus 2*) as well as numerous papers on *Eucalyptus*. The first set of her collections, and those of D.J.Carr, were deposited at FRI (now transferred to CANB), with duplicates in several other Australian collections including AD, ADW (now AD), NT (now DNA) and PERTH.

References: Hall, 1978, 1989; Carr, 1989.

Carrick, John

Born in Glasgow, Scotland, on 14 June 1914, died in Adelaide, South Australia, on 4 January 1978.

After many years in Canada and several Asian countries, he joined the staff of the State Herbarium of South Australia in 1968. He specialised in studies of Lamiaceae, subfam. Prostantheroideae (particularly *Prostanthera*) and *Melaleuca*. His Australian collections are in AD, with duplicates distributed as exchange to many herbaria.

References: Anonymous, 1978, 1979a.

Portrait: Anonymous, 1979a.

Cavanilles, Antonio José

Born in Valencia, Spain, on 16 January 1745, died in Madrid, Spain, on 4 May 1804.

Spain's leading taxonomic botanist in the 18th century; in Paris 1777–1781; in Madrid 1789–1804; from 1801 Director of the Royal Botanic Gardens, Madrid. Described a number of Australian plants, including the genera *Angophora* and *Bursaria*, in his 6-volume *Icones et Descriptiones Plantarum...* (1791–1799). The Australian descriptions were based on collections made near Port Jackson and Botany Bay (New South Wales) by Luis Née (*q.v.*). Other Australian taxa were described in papers in *Anal. Hist. Nat.* 1: 89–107 (1799) & 3: 181–245 (1800). His main herbarium is at MA, with lesser amounts in BM, C, G, LD, LINN, MO, P, P-JU, P-LA and UPS.

References: Cameron, 1955; Daniels & Stafleu, 1972; Hall, 1978.

Portrait: Daniels & Stafleu, 1972.

Cheel, Edwin

Born in England on 14 January 1872, died in Sydney, New South Wales, on 19 September 1951.

Cheel worked as a gardener in Queensland and New South Wales, and was appointed to the staff of Centennial Park in 1897, before transferring to the Sydney Botanic Gardens. He joined the staff of the National Herbarium of New South Wales in 1908, becoming Chief Botanist and Curator (1933–1936). His main interests were in Myrtaceae and lichens, and he collected extensively, his collections being lodged in NSW.

Reference: Hall, 1978.

Chippendale, George McC.

Born in Sydney, New South Wales, on 18 April 1921.

Worked at the National Herbarium of New South Wales from 1936 until 1954, before being appointed first resident taxonomist in the Northern Territory Administration (1954–1966). He was responsible for laying the foundations of the Northern Territory Herbarium at Alice Springs (NT). From 1966–1983 he was Botanist/Senior Research Scientist with the Forest Research Institute (now CSIRO Forestry and Forest Products) in Canberra. He is noted in particular for his work on *Eucalyptus*, having published a number of books on the subject (*Eucalyptus Buds and Fruits* (1968), *Eucalypts of the Western Australian Goldfields and Adjacent Areas* (1973) and *Flora of Australia Vol. 19 Myrtaceae — Eucalyptus, Angophora* (1988)). He also prepared a *Check List of Northern Territory Plants* (1972), a handbook on fodder trees and shrubs of the Northern Territory (1960), and contributed to the updating of several forestry handbooks. His main herbarium is to be found in CANB and DNA, with duplicates in many other institutions.

References: Hall, 1978, 1989; Chippendale 1992.

Partial Itineraries: Chippendale, 1992, 1996a.

Churchill, David M.

Born in Merredin, Western Australia, in 1933.

After an academic career, David Churchill was appointed Director of the Royal Botanic Gardens and Government Botanist of Victoria from 14 April 1971 until 1985, when these positions were replaced by managers. He retired on 9 March 1991. His research interests ranged from taxonomic studies on *Borya* to pollen, diatoms and vegetation surveys. His herbarium is housed at MEL.

Reference: Aston, 1991.

Portrait: Aston, 1991.

Cleland, John B.

Born in Norwood, South Australia, on 22 June 1878, died in Adelaide, South Australia, on 11 August 1971.

Qualified in medicine at Sydney University, New South Wales; served at London School of Tropical Medicine, at London Hospital (1903–1905); as Government Pathologist and Bacteriologist in Western Australia (1905–1909); as Principal Pathologist in New South Wales (1909–1920); and finally as Professor of Pathology at the University of Adelaide, South Australia (1920–1948). He had a lifelong interest in anthropology, ornithology and botany. He collected widely, often with Eric Sims, and others, and published numerous papers in all his fields of interest. In 1934 and 1935 he published *Toadstools and Mushrooms and other Larger Fungi of South Australia* Parts 1 & 2, for many years the most comprehensive Australian texts on macrofungi. However, he also collected vascular plants widely and his herbarium was presented to the University of Adelaide (ADU). It was transferred on permanent loan to AD in 1954. Other specimens can be found in A, MEL and NSW.

References: Eardley, 1959; Hansford, 1959; Southcott, 1971; Hall, 1978; Kraehenbuehl, 1983c, 1986; Barker, 1991a, 1991b.

Portraits: Southcott, 1971; Kraehenbuehl, 1986; Barker, 1991a.

Partial Itineraries: Barker, 1991a.

Clemens, Mary S.

Born in New York, U.S.A., in 1873, died in Chermside, Brisbane, Queensland, on 13 April 1968.

Accompanied her husband to the Philippines (1905–1907), later visiting and collecting in China, Indo-China, Borneo, Java and Singapore. She also collected in New Guinea (1935–1941) before moving to Brisbane. For about the next 10 years she collected around Brisbane and as far north as Mackay, Maryborough, Ingham and Tully. Her tens of thousands of specimens are to be found in AHFH, B, BR, CAS, GH, L, MICH, RM, SING and US.

Reference: Langdon, 1981.

Portrait: Langdon, 1981.

Collie, Alexander

Born in Aberdeenshire, Scotland, on 2 June 1793, died at King George Sound, Western Australia, on 8 November 1835.

Naturalist with Captain Beechey on his voyage to the west coast of North America (1825–1828); naturalist with Lieutenant Preston on an expedition from Cockburn Sound to Geographe Bay, Western Australia (1829). He was Government Resident at King George Sound in 1831 and explored around Albany and French River, 1829–1832. Colonial Surgeon at Swan River 1833–1835. His main collection is in K, with duplicates at MO.

References: Maiden, 1909b; Cohen 1966; Hall, 1978.

Cowan, Richard S.

Born in Crawfordsville, Indiana, U.S.A., on 23 January 1921, died in Perth, Western Australia on 17 November 1997.

Taxonomist and bibliographer, who worked for much of his life at the New York Botanical Garden (1948–1957) and Smithsonian Institution (1957–1985). A leading proponent and supporter of *Index Nominum Genericorum*, and co-author with Frans Stafleu of *Taxonomic Literature* 2nd edn (TL-2). Retired to Perth, Western Australia in 1986, where he continued his lifetime interest in taxonomic studies of legumes, particularly Mimosaceae and Caesalpiniaceae. In Australia he contributed to *Flora of Australia* Volumes 11, 12 and 13 (*Acacia* and numerous genera in Caesalpiniaceae and Fabaceae), as well as publishing separately on *Acacia*. His collections are in A, BISH, GH, NY, PERTH, US and WAB.

References: Hall, 1993; Nicolson, 1998a, 1998b.

Cunningham, Allan

Born in Wimbledon, England, on 13 July 1791, died in Sydney, New South Wales, on 27 June 1839.

Selected by Banks from among Kew staff to be an overseas collector ('King's Botanist to the Royal Botanic Gardens Kew'). Between 1814 and 1816 he collected in Brazil, arriving in Australia in December 1816. Cunningham joined several expeditions, including that of Oxley along the Lachlan and Macquarie Rivers (1817) and Philip Parker King's coastal surveys (*Mermaid* and *Bathurst*, 1817–1822). In 1818 he collected at Illawarra, New South Wales, and in Tasmania at Hobart and Macquarie Harbour. Other localities visited by the King survey included Port Macquarie and Hastings River in New South Wales, Rodd's Bay, Percy Isles, Cleveland Bay, Halifax and Rockingham Bays, and Endeavour River in Queensland, and Goulburn Island, Vernon Islands, Cambridge Gulf and Port Wanderer in northern Australia. In 1822 Cunningham collected in New South Wales at Illawarra, Blue Mountains, Pandora Pass and Liverpool Plains. In 1824 he visited the source of the Murrumbidgee and Brisbane Rivers, and in 1825 the Nepean and Hunter Rivers, Pandora Pass, Liverpool Plains, Wellington Valley, Coxs River and other places in New South Wales. He was in New

Zealand (1826) and on the Darling Downs, Queensland (1827). He returned to England in 1831, but came back to New South Wales in 1837 as Government Botanist, a position he resigned after a year. Many taxa have been based on his collections, and many of his manuscript names have since been taken up, but he published little himself. His main collection is at K, with some duplicates elsewhere, including B, BM, BR, BRI, CGE, DBN, E, FI, G, GH, GL, L, LINN, M, MEL, MO, NSW, OXF (500+ specimens), SING, U, US, W and WELT.

References: Bailey, 1891; Froggatt, 1932; J.Willis, 1949a; Osborn, 1952; McMinn, 1970; Hall, 1978; Nelson, 1980; Gilbert, 1981; Finney, 1984; Gilbert, 1986; Barker & Barker, 1990; Curry & Maslin, 1990; Telford, 1990; Cohn & Almond, 1991; Olde & Marriott, 1994; Kenneally *et al*., 1996.

Portraits: Feeken *et al*., 1970; McMinn, 1970; Hall, 1978; Gilbert, 1981; Gilbert, 1986; Olde & Marriott, 1994; Kenneally *et al*., 1996.

Maps and lists of collecting localities: McMinn, 1970; Curry & Maslin, 1990.

Cunningham, Richard

Born in Wimbledon, England, on 12 February 1793, died near Dandaloo, New South Wales, about 15 April 1835.

Younger brother of Allan Cunningham. Worked on *Hortus Kewensis* around 1808, before travelling to Australia and New Zealand (1833–1834). Appointed Colonial Botanist (New South Wales) and Superintendent of Botanic Gardens, Sydney (1833–1835) on the recommendation of Robert Brown, Cunningham sent numerous live plants back to Ireland and England. Killed on Mitchell's second expedition. His collections are at K, with duplicates in E, GL, MEL, MO, NSW and OXF.

References: Maiden, 1908a; Froggatt, 1932; Gilbert, 1981, 1986; Nelson, 1990.

Portraits: Gilbert, 1981, 1986.

Curtis, Winifred M.

Born in London, England, on 15 June 1905.

Came to Tasmania in September 1939, and almost immediately joined the Biology Department of the University of Tasmania, only the second woman to be appointed to the University staff. In 1945 she was a foundation member of staff of the Botany Department, eventually rising to the position of Reader, with several periods as Acting Head of Department. Her initial research on chromosome numbers (*Dianella*, *Pultenaea*) revealed the first reported case of polyploidy in the Australian flora (*Pultenaea juniperina*). In 1945 she began writing *The Students' Flora of Tasmania* as an aid to her teaching duties, and this task has continued until the present day, with a second edition underway. From 1967–1978 she contributed the text for the six volumes of *The Endemic Flora of Tasmania*, for which Margaret Stones prepared the plates. On retirement in 1966, she continued to take an active interest in the Tasmanian flora, and was instrumental in the establishment of the present Tasmanian Herbarium in 1977. Thirty years after retirement, Winifred is still visiting the herbarium several times a week, working on her *Students' Flora*. Since 1970 she has been assisted in this by Dennis Morris. In 1991 the Royal Society of Tasmania published a commemorative volume to mark her 85th birthday (see Kantvilas, 1991). Her main herbarium collections are housed in HO, with a substantial number of duplicates in K. Other duplicates are to be found in AD, CANB, MEL, NSW and some other herbaria.

Reference: Kantvilas, 1991.

Portrait: Kantvilas, 1991.

Dallachy, John

Born in Morayshire, Scotland, about 1808, died near Cardwell, Queensland, on 4 June 1871.

A gardener for the Earl of Aberdeen and later at Kew, Dallachy went to Ceylon as a plantation manager in 1847. Appointed Superintendent of the Melbourne Botanic Garden, Victoria, 1849–1857. Thereafter an assiduous collector for Mueller, from 1857–1862 in Victoria, and from 1862–1871 in northern Queensland, particularly in the Rockingham Bay region. Some ambiguities in his citation of locality names were resolved by Blake (1954). His collections are now in MEL, with duplicates at B, BM, KIEL and W.

References: Blake, 1954; Hall, 1978; Willis & Cohn, 1993; Olde & Marriott, 1994.

Partial itinerary: Maiden, 1908b.

Map of collection localities: Blake, 1954.

Dampier, William

Born in East Coker, Yeovil, England, on 5 September 1652, died in London, England, in March 1715.

British navigator who collected plants in Brazil, Australia, Timor and New Guinea. He visited the Dampier Peninsula (landing point variously thought to be at Cygnet Bay or Karrakatta Bay) in north-western Western Australia in 1688 (*Cygnet*), but made no collections. He returned to collect at Shark Bay and in the Dampier Archipelago (? Lewis Island) for five weeks from 1 August 1699 (*Roebuck*). George (1971) has identified 23 species of Australian plants among the Dampier collections (c. 40 specimens) preserved in OXF (others are in BM).

References: Bailey, 1891; Maiden, 1909b; Osborn & Gardner, 1939; Feeken *et al*., 1970; George, 1971; Finney, 1984; Kenneally *et al*., 1996.

Portrait: Feeken *et al*., 1970.

Diels, F. Ludwig E.

Born in Hamburg, Germany, on 24 September 1874, died in Berlin, Germany, on 30 November 1945.

Between 1900 and 1902 he and Ernst Pritzel collected widely in South Africa, Java, eastern and Western Australia and New Zealand. They were in Western Australia from October 1900 to December 1901, and collected over 5700 specimens. Their joint publication *Fragmenta Phytographiae Australiae Occidentalis* (*Bot. Jahrb*. 35, 1905) is one of the milestones in the description of Western Australian plants. A translation of Diels' account of the exploration of the Western Australian flora appears in Diels (transl. Carr, 1981). His main collection, including many holotypes, went to B, but the Type collection was destroyed in an air raid on 2 March 1943. Duplicates (including isotypes) can be found in BM, MEL, NSW and PERTH.

References: Hall, 1978; Diels (transl. Carr), 1981; Short, 1990c; Olde & Marriott, 1994.

Dietrich, K. Amalie

Born in Siebenlehn, Saxony, on 26 May 1821, died in Hamburg, Germany, on 9 March 1891.

Sent to Brisbane, Queensland, in 1863 as a paid collector for the Godeffroy Museum in Hamburg, she spent the next 10 years making extensive plant, animal and anthropological collections. She was based for a time in Bowen, Brisbane, Gladstone, Mackay and Rockhampton, and travelled at least short distances inland. Her collections formed the basis of *Zur Flora von Queensland* by C.Luerssen (*J. Mus. Godeffroy* 3: 1–22 (1873) & 3: 233–254 (1875)) and of Domin's works (see below). Her main collection is housed at HBG, but a set of duplicates was presented to Domin. Of the new taxa published by Domin, the specimen at PR should be considered the holotype, that at HBG the isotype (Kanis, 1977). A number of duplicates are also in MEL, donated by HBG in the 1970s. Some others may have been sent to Mueller directly by Dietrich, and material is also in B, BM, BRSL, JE, K, L, MO, P, US and W.

References: Maiden, 1912; Kanis, 1977; Moyal, 1981; Vallance, 1983; Hall, 1984; Robson, 1988; Sumner, 1988, 1993; Jobson, 1995; Martin, 1996.

Portraits: Maiden, 1912; Sumner, 1988, 1993.

Itinerary: Sumner, 1993.

Domin, Karel

Born in Kutna Hora, Bohemia [now Czech Republic], on 4 May 1882, died in Prague, Czech Republic, on 10 June 1953.

Visited Queensland from December 1909 until April 1910 with the geologist Jíri Danes (see Hall, 1984, for biography) as part of an expedition to Java and Australia. Their itinerary extended from Cairns to Brisbane, and inland as far as Hughenden, Cloncurry, Winton and Longreach. Domin also briefly visited the Blue Mountains near Sydney, New South Wales. On his return he studied additional material in K (particularly the collections of Captain A.A.Dorrien Smith (south-western Western Australia) and Dr E.Clement (north-western Western Australia), see Hall, 1979, 1984) and GOET, and was given a set of Amalie Dietrich's Queensland collections. From these sources he published a series of important works on Australian taxonomy and phytogeography in *Repertorium specierum novarum regni vegetabilis* (1911–1913), *J. Linn. Soc., (Bot.)* (1912), and *Bibliotheca Botanica* Vols 85 and 89 (1913–1915, 1921, 1925–1930). Domin's main Australian collection of about 4000 specimens (including duplicates from Dietrich, Clement and perhaps others) is housed separately at PR. His non-Australian collections are at PRC. Some specimens (including some grass Types) are at K and L.

References: Kanis, 1977; Hall, 1978; Chapman, 1986; Simon, 1987; Chapman, 1990; Macfarlane, 1991; Olde & Marriott, 1994.

Portraits: Chapman, 1986, 1990.

Drummond, James

Born in Hawthornden, Scotland, in 1784, died in Perth, Western Australia, on 27 March 1863.

Curator of the Cork Botanical Gardens, Ireland, 1809–1828. Emigrated with his family to the Swan River Colony, Western Australia, in 1829, and earned part of his living by selling plant collections to overseas botanists, notably William Hooker (K) and John Lindley (CGE). His collections are now to be found in about 25 herbaria (including DBN, G, MANCH, OXF, P), the largest holdings being in K and MEL. A very large number of species from south-western Western Australia are described from his collections, with 119 being named after him. His private collection was acquired by gift or purchase by MEL from his son after his death, and other duplicates were acquired by MEL with the purchase of the Steetz and Sonder herbaria. In 1917 duplicates of the MEL Drummond collections were sent to PERTH.

References: Bailey, 1891; Maiden, 1909b; Osborn, 1952; Erickson, 1966, 1969; D.Perry, 1971; Nelson, 1980; Hamersley, 1981; Carr & Carr, 1981b; Hilton, 1983; Short, 1990a; Conn, 1994; Olde & Marriott, 1994.

Portraits: Erickson, 1969; Olde & Marriott, 1994.

Map of collecting localities: Erickson, 1969.

Dryander, Jonas C.

Born in Gothenburg, Sweden, on 5 March 1748, died in London, England, on 19 October 1810.

A pupil of Linnaeus, he arrived in London on 10 July 1777. Botanist/librarian to Banks from 1782, librarian of the Royal Society and Vice-President of the Linnean Society. Editor (and part writer) of Aiton's *Hortus Kewensis* (1st edn and part of 2nd edn), and author of a paper on Australian plants in *Ann. Bot. (König & Sims)* 2: 504–532, 1806. His herbarium is housed at BM.

References: Maiden, 1908a; Olde & Marriott, 1994.

Portrait: Mabberley, 1985.

Dumont d'Urville, J.S.C.

Born in Condé-sur-Noireau, France, on 23 May 1790, died in a train accident in France on 8 May 1840 (Maiden, 1910b, gives the latter date as 12 May 1842).

First visited Australia with Louis Duperrey in *Coquille*, staying at Port Jackson, New South Wales, for two months from 17 January 1824. His collecting included a trip to Bathurst, New South Wales. He later commanded a French exploring expedition to the Pacific in *Astrolabe* (*Coquille* renamed) in 1826–1829. The expedition called at King George Sound (Western Australia), Western Port (Victoria), Sydney (New South Wales) and Hobart (Tasmania), where collections were made by d'Urville and L.A.Lesson (better known as a zoologist). He commanded a third expedition in 1837–1840 (*Astrolabe* and *Zélée*), on which the botanists were J.B.Hombron, H.Jacquinot and E.J.F.LeGuillon. This expedition touched on northern Australia and also visited Hobart. Collections from these expeditions are now housed in P and PC, with lesser numbers in B, G, G-DC and W.

References: Maiden, 1910b; Finney, 1984; Cohn & Almond, 1991.

Portrait: Maiden, 1910b.

Maps of voyage: Bailey, 1891; Cohn & Almond, 1991.

Eardley, Constance M.

Born in Fullarton, South Australia, on 6 September 1910, and died there on 15 May 1978.

Held a joint appointment from June 1933 to 1949 as curator of the herbaria at the Waite Institute and the Botany Department, University of Adelaide, South Australia. She was lecturer in Systematic Botany at the University of Adelaide, halftime from 1943, fulltime from 1950, and was Senior Lecturer from 1966 until December 1971. She wrote the catalogue of plants for the Simpson Desert Expedition of 1939. Con Eardley conducted research on South Australian sphagnum bogs and swamp vegetation in 1943, moving on to arid zone plants, and cytology, in later years. She was instrumental in training a generation of taxonomists in Adelaide, inspiring them with her enthusiasm. Her herbarium was lodged at ADU and ADW, both since transferred to AD.

References: Lange *et al.*, 1978; Kraehenbuehl, 1983c, 1986; Hall, 1984; Gardner, 1990.

Portraits: Kraehenbuehl, 1986; Gardner, 1990.

Eichler, Hansjoerg

Born in Ravensburg, Germany, on 1 April 1916, died on a visit to Berlin, Germany, 22 June 1992 (resident in Canberra, Australian Capital Territory).

Educated in Germany, at the University of Berlin and the University of Halle-Wittenberg. A protégé of Professor Diels, Eichler worked at the Botanisches Museum Berlin-Dahlem (1936–1943) and the Kaiser-Wilhelm-Institut für Kulturpflanzenforschung in Vienna and Gatersleben (1944–1945). In November 1955 he took up the position of first Keeper of the

State Herbarium of South Australia (AD), and in 1973 was appointed as Curator of Herbarium Australiense (CANB), Australian Capital Territory, where he remained until his retirement in 1981. His first herbarium of European specimens was destroyed by war action on 1 March 1943. His second herbarium, of 12 000 specimens from Germany, the Alps, Hungary, the Crimea, Daghestan and Sicily is housed mainly in GAT and HAL, with some also in AD and CANB. His third and largest herbarium of over 20 000 specimens, from all States of Australia (with a few specimens from New Zealand and Papua New Guinea), is housed in AD and CANB, with duplicates in many herbaria around the world. Eichler had a strong lifelong interest in nomenclature and served on several international nomenclatural committees. His taxonomic interests centred on *Hydrocotyle*, Ranunculaceae and Zygophyllaceae, but extended to many other groups, exemplified by his landmark *Supplement to Black's Flora of South Australia* and *Corrigenda* (Eichler 1965, 1966).

References: Hall, 1978; Conn *et al*., 1981; Robertson, 1993; Schodde, 1993; Orchard, 1995.

Portrait: Orchard, 1995.

Endlicher, Stephan L.

Born in Pressburg (now Bratislava, Slovakia), on 24 June 1804, died in Vienna, Austria, on 28 March 1849.

Initiator (with Martius) of *Flora Brasiliensis*, and author of a number of works describing Australian plants, of which the most notable are probably *Prodromus Florae Norfolkicae* (1833), *Genera Plantarum* (1836–1840), *Enumeratio Plantarum... Hügel* (1837), *Stirpium Australasicum... Hügeliani* (1838) and *Enchiridion Botanicum* (1841). His Types and main collection are at W with other specimens at P.

References: Maiden, 1908a; Hall, 1978; Olde & Marriott, 1994.

Portrait: Olde & Marriott, 1994.

Evans, Obed D.

Born in Redfern, New South Wales, in 1889, died in Sydney, New South Wales, on 26 July 1975.

Laboratory Attendant/Senior Laboratory Attendant at the Botany School, University of Sydney (1916–1954) where he was largely responsible for the development of the John Ray Herbarium (SYD). From April 1959 until June 1971 a part-time botanist at NSW. Co-author of the *Flora of the Sydney Region* (1963, 1972, 1982), nine research papers and accounts of eight families for *Flora of New South Wales (Contr. New South Wales Natl. Herb.)*. His collections are to be found at SYD and NSW (duplicates in S and elsewhere).

References: Carolin & Johnson, 1976; Johnson, 1976.

Portrait: Carolin & Johnson, 1976.

Everist, Selwyn L.

Born in Tewantin, Queensland, on 22 April 1913, died in Brisbane, Queensland, on 21 October 1981.

After working as a botanist in western Queensland, particularly in the Blackall region, from 1936, Everist was appointed Government Botanist for Queensland 1954–1971, succeeding W.D.Francis, and Director, Botany Branch and Queensland Herbarium from 1971. He retired on 2 July 1976. Throughout his career his major interest was in economic botany, with particular emphasis on weeds and poisonous plants. His book *Poisonous Plants of Australia* (1974, 1981) remains the classic work in this field. Under his direction, the Queensland Herbarium was among the first to embark on electronic databasing of its label data. His collections are housed in BRI, with some also in A, LCU and MO.

References: Johnson, 1981; Everist, 1982; Hall, 1984.

Portrait: Johnson, 1981.

Ewart, Alfred J.

Born in Liverpool, England, on 12 February 1872, died in East Malvern, Victoria, on 12 September 1937.

Arrived in Victoria in 1906 to take up the dual position of Government Botanist and Professor of Botany at the University of Melbourne. He relinquished the former position in 1921. His research interests spanned both plant physiology and taxonomy, and under his leadership the MELU herbarium was established and fostered. He is perhaps best remembered for his *Flora of Victoria* published in 1931, but was also the author of many papers and other books, including *Handbook of Forest Trees for Victorian Foresters* (1925), *Weeds, Poison Plants, and Naturalised Aliens of Victoria* (with J.R.Tovey, 1909) and *The Flora of the Northern Territory* (with O.B.Davies, 1917). His main collections are at MEL, with a few duplicates elsewhere, including B, DBN and NH.

References: J.Willis, 1949a; Hall, 1978; Nelson, 1980; Chambers, 1981; I.Clarke, 1990; Willis & Cohn, 1993; Olde & Marriott, 1994; Short, 1997b.

Portrait: Willis & Cohn, 1993.

Eyre, Edward J.

Born in Whipsnade, Bedfordshire, England, on 5 August 1815, died near Tavistock, England, on 30 November 1901.

Leader of an expedition from South Australia to Western Australia in 1840–1841. Collections were made from the lower Flinders Range, Eyre Peninsula and across the Great Australian Bight to Albany. At least some of these specimens are now in MEL, although Maiden (1908c) reported that the earlier collections were lost.

References: Maiden, 1908c; Feeken *et al*., 1970; Kraehenbuehl, 1986.

Portraits: Feeken *et al*., 1970; Kraehenbuehl, 1986.

Fitzalan, Eugene F.A.

Born in Londonderry, Ireland, on 12 July 1830, died in South Brisbane, Queensland, on 22 June 1911.

A trained gardener and nurseryman, Fitzalan came to Victoria in 1849, moving to Queensland in 1859. He was botanical collector on Lieutenant J.W.Smith's 1860 expedition to the north-eastern coast, which resulted in the establishment of Bowen. Fitzalan collected 130 specimens on this expedition. He later settled at Bowen, moving to Cairns in 1887. He sent material to Mueller over many years, and many of his collections are cited by Bentham. His herbarium is in MEL.

References: Maiden, 1921; Hall, 1978.

Portrait: Maiden, 1921.

Fitzgerald, Robert D.

Born in Tralee, Ireland, on 30 November 1830, died in Hunters Hill, New South Wales, on 12 August 1892.

Arrived in Sydney, New South Wales, in 1856. Employed at the Surveyor-General's office, eventually becoming Deputy Surveyor-General. Noted for the production of *Australian Orchids* (1875–1894), from his own illustrations, lithographed by A.J.Stopps. He had no substantial herbarium, but a few of his collections are in BM and MEL. Many of his original drawings (100+) are held in the National Library of Australia, Canberra.

References: Maiden, 1908a; Gilbert, 1985.

Portrait: Gilbert, 1985.

Fitzgerald, William V.

Born in Mangana, Tasmania, on 21 July 1867, died on the Daru River, New Guinea, on 6 August 1929.

He collected in Tasmania, New Guinea and Western Australia, his most important expeditions being to the Kimberley region, Western Australia, in 1905 and 1906 (results published in 1916 and 1918). He described five genera and about 210 species from Western Australia (Short, 1990c). His specimens are now in B, E, HO, MEL, NH, NSW and PERTH.

References: Hall, 1978; Kenneally, 1986; Short, 1990c, 1993; Hall, 1993; Maslin & Cowan, 1994a; Olde & Marriott, 1994; Kenneally *et al*., 1996.

Species lists: Kenneally, 1986.

Flecker, Hugo

Born in Prahran, Victoria, on 7 December 1884, died in Cairns, Queensland, on 25 June 1957.

A medical practioner in Melbourne, Victoria, Flecker moved to Cairns in 1932, where he became foundation President of the North Queensland Naturalists' Club. Over the next 25 years he built, with the Club, an herbarium of nearly 11 000 collections (CAIRNS). This herbarium was incorporated into QRS in 1971, with the bryophytes going to CANB in 1981.

References: Hall, 1984; Clarkson, 1990.

Portrait: Clarkson, 1990.

Foelsche, Paul H.M.

Born in Moorburg, Germany, on 30 March 1831, died in Darwin, Northern Territory, on 31 January 1914.

A member of the South Australian police from about 1853, transferring to the Northern Territory in 1870, where he was Inspector of Police at Palmerston for many years. He collected in the Territory, sending material to F.Mueller. These collections are now in MEL.

References: Maiden, 1921; Hall, 1978.

Portrait: Maiden, 1921.

Forrest, John

Born in Bunbury, Western Australia, on 22 August 1847, died at sea, on 3 September 1918.

In 1869 he led an expedition in search of Leichhardt, and in 1870 led another from Perth (Western Australia) to Adelaide (South Australia) around the Great Australian Bight. Apparently neither of these involved plant collecting. In 1874 he crossed the Great Victoria Desert from Champion Bay, Western Australia, to the Overland Telegraph Line in the Northern Territory. The botanical collections from the latter expedition were sent to Mueller and are now in MEL. Forrest later became Deputy Surveyor-General for Western Australia, held other government posts, and became the first Premier and Colonial Treasurer of Western Australia. After 1901 he held ministerial posts in the Federal Government, including Acting Prime Minister.

References: Feeken *et al.*, 1970; Hall, 1978; Kraehenbuehl, 1986; Cohn & Almond, 1991; Olde & Marriott, 1994.

Portraits: Feeken *et al.*, 1970; Kraehenbuehl, 1986.

Map of 1873–1874 expedition: Cohn & Almond, 1991.

Forster, J. George A.

Born in Nassenhuben near Gdansk, Poland, on 26 November 1754, died in Paris, France, on 11 January 1794.

Son of J.R.Forster, accompanying him on his voyage (see below).

Forster, Johann R.

Born in Tczew near Gdansk, Poland, in 1729, died in Halle, Germany, on 9 December 1798.

With his son, botanist on Cook's second voyage (*Resolution* and *Adventure*) to the South Seas. The Forsters were aboard *Resolution*. Only the *Adventure* touched Australian shores, at Adventure Bay, Tasmania (February 1773). The Forsters wrote a number of (largely unauthorised) works on their voyage, describing some South Pacific plants which extend to Australia. Their herbarium was dispersed. Large numbers of specimens are at BM, LIV, UPS and W, smaller numbers at B, GOET, IAC, K, KIEL, L, LINN, LZ, MO, MW, P, PH and WELT.

References: Bailey, 1891; Maiden, 1908a; Carolin, 1963; Apfelbaum, 1971; Hoare, 1976; Finney, 1984; Olde & Marriott, 1994; Hansen & Wagner, 1998.

Portraits: Duyker & Tingbrand, 1995.

Francis, William D.

Born in Bega, New South Wales, on 6 March 1889, died at Kangaroo Point, Queensland, on 2 January 1959.

Appointed Assistant Government Botanist at the Queensland Herbarium in 1919, and promoted to Government Botanist in 1950 on the death of C.T.White, retiring in 1954. Perhaps best known for writing two editions of *Australian Rainforest Trees* (1929, 1951). His herbarium is at BRI, with duplicates in A.

References: Hall, 1978; Everist, 1982.

Fraser, Charles (sometimes 'Frazer')

Born in Blair Athol, Perthshire, Scotland, about 1788, died in Parramatta, New South Wales, on 22 December 1831.

Arrived in Port Jackson, New South Wales, in April 1816 as a soldier, later being appointed first Colonial Botanist and Superintendent of the Botanic Gardens. He was a member of Oxley's 1817 (Lachlan River, Bathurst), 1818 (north-eastern New South Wales) and 1819 (Port Macquarie/Hastings River) expeditions, visited Moreton Bay in 1828 at the request of the Governor to collect plants and form a public garden, and visited the Swan River district in Western Australia in 1827 as part of Stirling's pre-settlement survey. He also visited Tasmania (1820, 1826), and New Zealand and Norfolk Island (1826). Sponsored William Baxter's expedition to Western Australia in 1828–1829. His main collection is at K, with other material at A, BM, CGE, E, MO, NSW and OXF (500 specimens).

References: Maiden, 1908a; Froggatt, 1932; Osborn, 1952; Hall, 1978; Finney, 1984; Gilbert, 1986; Barker & Barker, 1990; Olde & Marriott, 1994.

Furneaux, Tobias

Born in Swilly, near Portsmouth, England, on 21 August 1735, and died there on 19 September 1781.

Commander of *Adventure* during James Cook's second voyage to the Pacific. Visited Adventure Bay, Bruny Island, in Tasmania for four days from 9 March 1773. Seeds and some specimens of *Leptospermum lanigerum* and seeds of *Eucalyptus obliqua* were collected, and the specimens (the earliest extant ones from Tasmania) are now in BM. Both species were grown in England from these seeds.

Reference: Nelson, 1981b.

Gardner, Charles A.

Born in Lancaster, England, on 6 January 1896, died in Subiaco, Western Australia, on 24 February 1970.

Appointed to the Western Australian Forests Department as a plant collector in 1920, Gardner transferred to the Department of Agriculture in 1924 as assistant to the Economic Botanist and Plant Pathologist. In January 1929 he became Government Botanist and Curator of the State Herbarium, a position he held until retirement in 1960. He published extensively on the Western Australian flora, the most important works being *Botanical Notes, Kimberley Division of Western Australia* (1923), the series *Contributions to the flora of Western Australia* in *J. [Proc.] Roy. Soc. W. Australia* from 1923, *Enumeratio Plantarum Australiae Occidentalis* (1930) and *Flora of Western Australia Vol. 1, part 1, Gramineae* (1952). Gardner was an enthusiastic collector, his first official expedition to the northern Kimberley in 1921 yielding 325 specimens. By 1946 he estimated his collections at 10 000 sheets. He described eight genera and about 200 species of Western Australian plants in about 320 publications. Gardner's personal herbarium was bequeathed to the Benedictine Community at New Norcia, but was transferred to PERTH in June 1970. Lesser numbers of specimens are in A, AIB, B, K, MEL and NSW.

References: D.Perry, 1971; Hall, 1978; Wilson, 1988; Green, 1990; Buehrig & Hooper, 1993; Olde & Marriott, 1994; George, 1996a; Chippendale, 1996b.

Portraits: Buehrig & Hooper, 1993; Olde & Marriott, 1994.

Gauba, Erwin

Born in Vienna, Austria, in 1891, died in 1964.

Professor of Botany at the University of Tehran until 1940s. After moving to Canberra, Australian Capital Territory, he became a close research associate of L.D.Pryor, and was appointed (Temporary) Botanist at the Canberra Botanic Gardens (later Australian National Botanic Gardens). He and Pryor amassed a substantial herbarium, much of which was later transferred to the Canberra University College (later Australian National University, GAUBA). Some specimens remained in CBG, and these are now in CANB. Gauba retired in 1960.

References: Court, 1980; Wrigley, 1980.

Gaudichaud-Beaupré, Charles

Born in Angoulème, France, on 4 September 1789, died in Paris, France, on 16 January 1854.

Botanist with Freycinet's expedition of 1817–1820 in *Uranie* and *Physicienne*. Collected in Western Australia at Shark Bay for two weeks in September 1818, and for two months (November–December 1819) in New South Wales at Port Jackson, Botany Bay, and the Blue Mountains. He also undertook an excursion to Bathurst. His collections, to be found in P, were described in the account of the voyage (*Voyage autour du Monde sur l'Uranie et la Physicienne*, 1826), and later by others. Duplicates may be in B, BR, DS, FI, G, G-DC, K, L, MO, PC, P-JU, US and W.

References: Bailey, 1891; Maiden, 1910b; Finney, 1984; Cohn & Almond, 1991; Olde & Marriott, 1994; Pearce, 1996.

George, Alexander S.

Born in Western Australia, on 4 April 1939.

A member of staff of the Western Australian Herbarium 1959–1981. From 1981–1993 foundation Executive Editor of the *Flora of Australia*. His research activities span Caesalpiniaceae, Myrtaceae, Orchidaceae and Proteaceae, and he is perhaps best known for work on *Banksia*, *Dryandra*, *Synaphea* and *Verticordia*. His main herbarium (17 000+ numbers) is in PERTH.

References: Hall, 1978; George *et al*., 1993; Olde & Marriott, 1994.

Portrait: George *et al*., 1993.

Gilbert, John

Born on 14 March, year unknown (possibly 1810), probably in England, killed at the Gulf of Carpentaria on Leichhardt's expedition to Port Essington, 28 June 1845.

An assiduous collector of birds and animals for Gould, but also collected some plants. Collected plants and other material for Gould in south-western Western Australia in 1840 and 1842. His herbarium is in BM, K and W.

References: Maiden, 1909b; Chisholm, 1966; Hall, 1978.

Giles, W. Ernest P.

Born in Bristol, England, on 20 July 1835, died in Coolgardie, Western Australia, on 13 November 1897.

Came to Australia in 1851. He conducted four major expeditions: in 1872 and 1873 to northern South Australia and Central Australia; in 1875 from Beltana via the Gawler Ranges, Ooldea and the Great Victoria Desert to Perth; and the return in 1876 through the Gibson Desert, Rawlinson Range and north-western South Australia. Botanical collectors on these expeditions were Christopher Giles (1872, 1873), and Jesse Young & W.H.Tietkens (1875, 1876). The collections from the expeditions were described by Mueller, and are in MEL, with some also in CANB, KIEL and P.

References: Maiden, 1908c; Feeken *et al*., 1970; Hall, 1978; Kraehenbuehl, 1986; Cohn & Almond, 1991; Olde & Marriott, 1994.

Portraits: Feeken *et al*., 1970; Hall, 1978; Kraehenbuehl, 1986.

Map of expeditions: Cohn & Almond, 1991.

Good, Peter

Place and date of birth unknown, died off Sydney, New South Wales, on 11 June 1803.

A gardener at Kew from at least 1796 until 1801. Visited India in 1796 to bring back to Kew a collection of plants formed by Christopher Smith. Appointed in 1801 to join Flinders' *Investigator* voyage as assistant to Robert Brown. Contracted dysentery at Timor, and died off Sydney, 11 June 1803. His collections were incorporated (unacknowledged) in Brown's own. A small number of specimens collected at Kew by William McNab, from plants raised from seed collected by Good during Flinders' voyage, are now in DBN.

References: Maiden, 1908a; Edwards, 1976, 1981a, 1981b; Nelson, 1980, 1981a; Finney, 1984; Clarkson, 1988; Barker & Barker, 1990; Grandison, 1990; Nelson, 1996.

Gosse, William C.

Born in Hoddesdon, England, on 11 December 1842, died in Adelaide, South Australia, on 12 August 1881.

Leader of an expedition to north-western South Australia and the Northern Territory, September–December 1873. Visited the Tompkinson, Mann, Musgrave and Everard Ranges, before moving on to Charlotte Waters (Northern Territory). His brother Henry was collector on the expedition. The specimens, now in MEL, were cited in Bentham, *Flora Australiensis*, and in Mueller's *Fragmenta*.

References: Feeken *et al*., 1970; Kraehenbuehl, 1986.

Portraits: Feeken *et al*., 1970; Kraehenbuehl, 1986.

Gray, Asa

Born in Sauquoit, New York, U.S.A., on 18 November 1810, died in Cambridge Massachusetts, U.S.A., on 30 January 1888.

Leading taxonomic botanist in the U.S.A. during the 19th century, and Fisher Professor of Natural History at Harvard from 1842. Never visited Australia, but described the plants of the *United States Exploring Expedition... under the command of Charles Wilkes* (1854), which visited Tasmania and Sydney, New South Wales, in 1839. The botanist on the voyage was W.D.Brackenridge. Gray's main herbarium and Types are at GH, but duplicates are widely scattered.

References: Bailey, 1891; Maiden, 1908a.

Green, John W.

Born in Waverley, New South Wales, on 10 July 1930.

Employed as Assistant Botanist in the Western Australian Herbarium by Charles Gardner (1954–1958) before taking up academic posts in Armidale, New South Wales (1958–1963), Canberra, Australian Capital Territory (1963–1966) and Canada (1970–1975), plus a period at the Forest Research Institute, Canberra (1966–1970). From 1975 to 1987 he returned to the Western Australian Herbarium as Curator, overseeing a period in which data-basing methods were introduced for collection management. His research interests covered *Conostylis*, variation in *Eucalyptus* spp, and Myrtaceae of the *Thryptomene* group. His collections are housed in PERTH.

References: Hall, 1978; Maslin, 1988a.

Gregory, Augustus C.

Born in Farnsfield, Nottinghamshire, England, on 1 August 1819, died in Brisbane, Queensland, on 25 June 1905.

Leader of the North Australian Exploring Expedition (1855–1857), which included Ferdinand Mueller. This expedition explored the Victoria River and Sturt Creek in the Northern Territory, before returning overland to Moreton Bay, Queensland. The collections from this expedition are in K and MEL. Gregory later led an expedition in search of Leichhardt (1857), along the Barcoo River (New South Wales) to Cooper Creek and Strzelecki Creek, arriving in Adelaide, South Australia, on 31 July 1858.

References: Hall, 1984; Kraehenbuehl, 1986; Cohn & Almond, 1991; Olde & Marriott, 1994; Cohn, 1996; Parkin, 1996a; Walsh, 1996.

Portrait: Feeken *et al*., 1970.

Grieve, Brian J.

Born in Allans Flat, Victoria, on 15 August 1907, died in Perth, Western Australia, 5 September 1997.

Educated in Williamstown, University of Melbourne, Victoria, and Imperial College, London, joining the staff of the Botany Department, University of Melbourne, in 1931. Moved to Western Australia from Victoria in 1947 as foundation Head of Botany at the University of Western Australia, becoming Professor of Botany in 1957. His research spanned ecophysiology, mycology, bacterial and viral plant infections, and rehabilitation of mine sites. Taxonomically, his major contribution was in taking over the work of W.E.Blackall, to produce, in several editions, the innovative illustrated key to the flora of Western Australia's south-west, *How to Know Western Australian Wildflowers*.

References: Anonymous, 1979c; Amalfi, 1997; Atkins, 1997.

Portraits: Anonymous, 1979c; Amalfi, 1997.

Gunn, Ronald C.

Born at Cape of Good Hope, South Africa, on 4 April 1808, died in Launceston, Tasmania, on 13 March 1881.

Arrived in Tasmania on 5 February 1830, and rapidly gained a series of government posts. Later managed the estates of W.E.Lawrence and of Lady Jane Franklin. Recruited by Robert Lawrence to send plant specimens to William Hooker at Kew. From 1832–1860 Gunn sent Hooker many hundreds of specimens from most parts of Tasmania. He also made several visits to Victoria. Gunn was a close associate of (and worked for) Governor Sir John and Lady Franklin, and hosted botanists such as W.H.Harvey, J.D.Hooker and Dumont d'Urville during their visits to Hobart. Gunn gathered around him a keen group of local naturalists including Mary Ballantine, William Breton, Richard Davies, John Lillie, John Robertson, Charlotte Smith and John Smith (see Buchanan, 1988b, 1990). Collections made by these persons and others (e.g. the convict servants James Lee and George Moran) were also forwarded to the Hookers. He presented his collection to the Royal Society of Tasmania in 1876 (?or 1878), and it was housed in the Tasmanian Museum. Much of this collection was transferred to NSW for safekeeping in about 1904. A set of duplicates and other material was subsequently returned to HO. Gunn's collections are thus to be found in K (specimens sent to the Hookers), and NSW (Gunn's main personal collection), with other large numbers in BM, CGE (distributed by the Hookers to Lindley) and HO. Osborn (1952) noted 1000 Gunn specimens in OXF. Small numbers of specimens are found elsewhere, including B, BRSL, C, CO, CN, F, FI, G, G-DC, GH, K, KIEL, L, LE, M, MEL, MO, P, S, TCD, US, W and WAG.

References: Maiden, 1909a, 1912; J.Willis, 1949a; Osborn, 1952; Burns & Skemp, 1961; Hall, 1978; Haegi, 1982; Buchanan, 1988a, 1988b; Lander, 1988b; Buchanan, 1990; Ducker, 1991.

Portraits: Maiden, 1912; J.Willis, 1949a; Buchanan, 1988b; Ducker, 1991.

Maps and lists of collecting localities: Buchanan, 1988b, 1990.

Hall, Norman

Born in Pahiatua, New Zealand, on 10 January 1906.

Worked in various Forestry organisations in New Zealand, South Australia, Scotland and New Guinea (during World War II), and the Australian Capital Territory. Perhaps best known as co-author of *Forest Trees of Australia* which appeared in four editions (1957, 1962, 1970, 1984). Another very important series of publications, *Botanists of the Eucalypts* (1978, Supplements in 1979, 1989, 1992), and *Botanists of Australian Acacias* (1984, Supplement in 1993), provide a comprehensive collection of biographies of Australian botanists and collectors.

References: Hall, 1978; Hall, 1993; Ingram, 1993.

Hannaford, Samuel

Born in Totnes, Devonshire, England, in 1828, died in Hobart, Tasmania, on 3 January 1874.

Arrived in Melbourne, Victoria, in 1853 and worked as a bank teller in Warrnambool (1855–1856) and Geelong (1856–1863). Moved to Tasmania in 1863. Editor of the *Victorian Agricultural & Horticultural Gazette* during his time in Geelong, and later editor of the *Launceston Times* (1863–1868), moving to Hobart from 1868. He wrote extensively on botany and agriculture, and collected throughout his time in Australia, including cooperation with John Fereday to collect algae at Tamar Heads for Harvey. His terrestrial collections are in HO, MEL and NSW.

References: Maiden, 1908b, 1909a; Willis & Cohn, 1993.

Portrait: Willis & Cohn, 1993.

Helms, Richard

Born in Altona, Germany, on 12 December 1842, died in Sydney, New South Wales, on 17 July 1914.

First arrived in Australia in 1858, subsequently living in New South Wales, Victoria, Western Australia and New Zealand, variously employed as a dentist, watchmaker, museum curator, collector, entomologist, fruit inspector and bacteriologist. As well as plants he formed extensive collections of beetles, butterflies and shells. He participated in a major collecting expedition to Mt Kosciuszko in 1888, visiting there again in 1893 and 1901, and was naturalist on the Elder Exploring Expedition to central Australia, May 1891–June 1892. The majority of the Elder Exploring Expedition specimens are now in AD, but some can also be found in A, C, CANB, G, K, M, MANCH(?), MEL, MO, NSW and OXF.

References: Maiden, 1908c; Hedley, 1915; Maiden, 1921; Anonymous, 1950b; Hall, 1978; Vallance, 1983; Kraehenbuehl, 1986.

Portraits: Maiden, 1921; Hall, 1978.

Itinerary: Anonymous, 1950b.

Herrgott, Joseph F.A.D.

Born in Scheslitz, Bavaria, in 1823, died in Melbourne, Victoria, on 8 October 1861.

Botanist on Babbage's expedition to northern South Australia in 1858 and on Stuart's 1860 expedition to central Australia. Plants from these expeditions were described by F.Mueller, although little credit was given to Herrgott. Hergott [sic] Springs is named after him. His collections are now in K and MEL.

Reference: Maiden, 1908c.

Hill, Gerald F.

Born in Melbourne, Victoria, in 1880, died in Sydney, New South Wales, on 18 January 1954.

Perhaps better known as an entomologist/zoologist, Hill was an all-round naturalist and collector. He collected in north-western Australia in 1909–1910, and in 1911–1912 was a member of Captain H.V.Barclay's expedition to the Macarthur River and the Gulf of Carpentaria. These latter collections formed much of the basis for Ewart & Davies' *The Flora of the Northern Territory* (1917). Hill's collections were acquired by Ewart through both donation and purchase, and are now at MEL, with duplicates in NSW.

References: Gay, 1954; Hall, 1978; Short, 1990c; Olde & Marriott, 1994.

Hill, Walter

Born in Scotsdyke, Scotland, on 31 December 1820, died in Canobie Lea, Eight Miles Plain, Queensland, on 4 February 1904.

Appointed first Superintendent of the Brisbane Botanic Gardens in 1855, and first Colonial Botanist of Queensland in 1859. He retained these positions until 1881. Hill undertook expeditions to Cape York (1862) and along the north-east coast to Mossman and the Daintree (1873), climbing Mt Bellenden-Ker. He developed a small herbarium and laid the basis of a botanical library. The herbarium was largely lost to termites and damp, although a few specimens survive in BRI, and duplicates exist in FI, K and MEL.

References: Maiden, 1910a; Hall, 1978; Everist, 1982; Olde & Marriott, 1994.

Holtze, Maurice W.

Born in Hanover, Germany, on 8 July 1840, died on Kangaroo Island, South Australia, on 12 October 1923.

Emigrated to Australia in 1872; Government gardener at Palmerston (Darwin), 1878–1891; later Director, Botanic Garden of Adelaide, South Australia. Holtze collected for Mueller: his specimens are in MEL (perhaps also in NSW?).

References: Maiden, 1908c; Kraehenbuehl, 1983a, 1986; Ruediger, 1988; Gibson, 1990a.

Portraits: Ruediger, 1988.

Holtze, Nicholas

Born in Bunsk, Russia, in 1867, died in Darwin, Northern Territory, on 24 May 1913.

Son of M.W.Holtze, and educated in South Australia. Curator of Darwin Botanic Gardens, 1891–1913. Specimens in MEL.

References: Maiden, 1908c; Ruediger, 1988; Gibson, 1990b.

Portraits: Ruediger, 1988.

Hoogland, Ruurd D.

Born in Leeuwarden, Netherlands, in 1922, died in Paris, France, on 18 November 1994.

From 1952 to 1968 a botanist with the New Guinea Group of CSIRO Division of Land Research and Regional Survey; from 1968 to 1979 a Research Fellow at the Australian National University's Research School of Biological Sciences, Australian Capital Territory. As well as collecting extensively in New Guinea, he visited Norfolk Island several times and Lord Howe Island once, and was an authority on their floras. Hoogland laid the foundations for the acquisition of the taxonomic library at CANB in the 1950s and 1960s. His major taxonomic research was undertaken on Dilleniaceae and Cunoniaceae. His main herbarium is in CANB; duplicates of his New Guinea herbarium are in A, BISH, BM, BO, BRI, G, K, L, LAE, MEL, NSW, PNH and US.

References: van Steenis-Kruseman, 1958; Orchard, 1994; Craven, 1995.

Portraits: van Steenis-Kruseman, 1958; Orchard, 1994.

Itineraries (Malesia): van Steenis-Kruseman, 1958.

Hooker, Joseph D.

Born in Suffolk, England, on 30 June 1817, died in London, England, on 10 December 1911.

Son of William Hooker, Assistant Director of Kew under him (1855–1865), and Director (1865–1885). In 1839 he joined Sir James Clark Ross' Antarctic expedition in *Erebus* and *Terror*. These ships explored the southern part of South America, New Zealand, and many islands of the South Pacific, as well as the subantarctic. They spent nearly six months in Tasmania, August–November 1840 and April–July 1841, as well as visiting Sydney, New South Wales, for three weeks in 1841. Hooker collected in the Hobart and Port Arthur areas and the upper Derwent in 1840, and in the Richmond and Huon areas in 1841. The outcome, the 6-volume *Botany of the Antarctic Voyage...*, provided the best account of the plants of New Zealand (*Flora Novae-Zelandiae*, 1852–1855) and Australia (*Flora Tasmaniae*, 1855–1859) written until that time. *Flora Tasmaniae* also contains a milestone essay on biogeography. Hooker later went on to explore in the Himalayas. His main collection is in K, but a few duplicates are held elsewhere, e.g. in BR, CAL, DBN, E, GH, HO, K, KATH, MANCH, MH, TCD and W. The *Erebus* and *Terror* specimens are in at least 31 herbaria.

References: Huxley, 1918; Turrill, 1963; Hall, 1978; Buchanan, 1988b; Cohn & Almond, 1991; Olde & Marriott, 1994.

Portraits: Huxley, 1918; Turrill, 1963; Mabberley, 1985.

Hooker, William J.

Born in Norwich, England, on 6 July 1785, died in London, England, on 12 August 1865.

Although without formal botanical training, William Hooker became one of the most influential British botanists of his time. Managed a brewery before becoming Professor of Botany at Glasgow University (1820–1840). After the death of Banks, Kew Gardens was allowed to sink into decline. The appointment of William Hooker as its Director in 1841 revitalised the gardens and herbarium. Hooker (and his son) recruited correspondents and collectors throughout the world. In Australia, Lawrence and Gunn in Tasmania, Drummond in Western Australia, Mueller and Adamson in Victoria, and others, sent copious material to Kew. Hooker published tirelessly, including many descriptions of Australian plants, particularly in the journals which he edited, *Botanical Miscellany* and *The Journal of Botany*. His herbarium is housed at K, with some duplicates elsewhere, e.g. LINN and LIV.

References: Stearn, 1965; Hall, 1978; Cohn, 1989; Olde & Marriott, 1994.

Portrait: Mabberley, 1985.

Howitt, Alfred W.

Born in Nottingham, England, on 17 April 1830, died in Bairnsdale, Victoria, on 7 March 1908.

Led the main relief expedition which discovered the bodies of Burke and Wills in September 1861. On a subsequent expedition (1861–1862) to recover their remains, he collected in north-eastern South Australia, south-western Queensland and western New South Wales. His collections were sent to Mueller and are now in MEL.

References: Willis, 1962; Hall, 1978; Kraehenbuehl, 1986.

Hügel, Baron Karl (sometimes Carl) A.A. von

Born in Regensburg, Germany, in 1795, died in Brussels, Belgium, in 1870.

Trained in law, and briefly a soldier, Hügel devoted his life from 1824 to the study of natural history, particularly botany and horticulture. In 1830 he embarked on a 6-year tour of India, Ceylon, Australasia, the Philippines and back to India and Kashmir. He visited the Swan River colony (Western Australia), including King George Sound, from 27 November 1833 until 11 January 1834, collecting extensively. The collections were described by Endlicher *et al*. in *Enumeratio Plantarum Novae Hollandiae* (1837) and *Stirpium Australasicarum Herbarii Hügeliana Decades Tres* (1838). In January and February 1834 he visited Tasmania, and then between April and October visited New South Wales twice, New Zealand and Norfolk Island. None of these eastern visits seem to have yielded collections. An extensive 2000-page diary of his Australian travels (with English translation by Ducker & Clark) is held by the Mitchell Library. A translation of most of this was published by Clark (1994). Hügel's collections are held by W, with duplicates in BR, CGE, CN, HBG, K, LE, M and MEL.

References: Maiden, 1909b; Hall, 1978; Hamersley, 1981; Vallance, 1983; Ducker, 1990; Clark, 1994; Olde & Marriott, 1994.

Portraits: Ducker, 1990; Clark, 1994; Olde & Marriott, 1994.

Maps of itineraries: Clark, 1994.

Hussey, Jessie L.

Born in Goolwa, South Australia, on 5 June 1862, died in Port Elliot, South Australia, on 16 March 1899.

Initially recruited by Mueller to collect marine algae in the Encounter Bay area of South Australia in 1893, she sent large numbers of both algae and terrestrial vascular plants to him, and algae to Agardh and other overseas phycologists. On her death, about 2000 of her specimens were deposited in the South Australian Museum, and these are (since 1957) in AD. Extensive collections are also in MEL, with others in BM, HBG, K and L.

References: Maiden, 1912; Kraehenbuehl, 1981b; Martin, 1996.

Ising, Ernest H.

Born in Norwood, South Australia, on 1 July 1884, died in Adelaide, South Australia, on 15 May 1973.

Worked for much of his life for the State railways, which enabled him to travel all over South Australia. He was a friend of Black who encouraged his interest in botany, leading Ising to collect a large herbarium between the 1920s and his death. His research concentrated on Chenopodiaceae, particularly the genus *Bassia* (now *Sclerolaena*). He also published on *Kochia* (*Maireana*), *Atriplex* and other taxa, describing 53 species or varieties in all. His herbarium is at AD (some received via the Museum collection, others directly), with duplicates elsewhere (e.g. E, K).

References: Kraehenbuehl & Campbell, 1975; Hall, 1978; Kraehenbuehl, 1983c, 1986.

Portrait: Kraehenbuehl, 1986.

Johnson, Lawrence (Lawrie) A.S.

Born in Cheltenham, New South Wales, on 26 June 1925, died in Sydney, New South Wales, on 1 August 1997.

Joined the staff of the National Herbarium of New South Wales in 1948; Deputy Chief Botanist (1968–1972); Director and Chief Botanist (1972–1985); Honorary Research Associate and Director Emeritus (1986–1997). Johnson worked on many major groups, but is perhaps best known for his work on *Eucalyptus*. With Pryor he wrote *A Classification of the Eucalypts* (1971). He has also provided new classifications for cycads and Casuarinaceae, wrote major morphological and phylogenetic overviews of Myrtaceae and Proteaceae with Barbara Briggs, and worked on *Juncus* (with Karen Wilson), Oleaceae, Restionaceae (with Briggs) and Zamiaceae among others. He took a leading role in discussions of nomenclature. Issue 6(4) of *Telopea* (1996) was dedicated to him, to mark his 70th birthday. His original collections are housed at NSW, with duplicates in BRI, K, MO and elsewhere.

References: Hall, 1978, 1989; Olde & Marriott, 1994; Anonymous, 1996; Benson, 1996; Briggs, 1996; Hull, 1996; Anonymous, 1997; Briggs, 1997.

Portraits: Olde & Marriott, 1994; *Telopea* 6(4), frontispiece, 1996; Anonymous, 1997.

Johnston, Robert M.

Born in Connage, Scotland, on 27 November 1844, died in Hobart, Tasmania, on 20 April 1918.

Registrar General and Government Statistician of Tasmania for many years; wrote extensively on Tasmanian geology and natural history, including plants. A few of his collections are in HO, others may be at MEL.

References: Maiden, 1921; Hall, 1978.

Kanis, Andries (Andrew)

Born in Alphen aan den Rijn, Netherlands, in 1934, died in Canberra, Australia, on 9 August 1986.

After work at Leiden and Sabah, Andrew Kanis joined the Taxonomy Group of the New Guinea Resources Section, CSIRO Division of Land Research, A.C.T. in 1969. In 1973 this group transferred to the Division of Plant Industry as part of Herbarium Australiense (now

Australian National Herbarium, CANB). He is best remembered for research on Amaranthaceae, Mimosaceae and Ochnaceae. Since his death, work on Amaranthaceae has been continued by Jo Palmer. He was also an accomplished nomenclaturalist who took an active interest in the *International Code of Botanical Nomenclature*. His main collections are at CANB.

Reference: Eichler, 1986.

Kempe, F.A. Hermann

Born in Deuben, Saxony, on 26 March 1844, died in Tanunda, South Australia, on 8 March 1928 (?1929).

Sent to the Northern Territory to establish a mission at the Finke River, he arrived in Adelaide, South Australia, in 1875. He was based at the Hermannsburg Mission from 1877 until 1893. During this time he sent about 600 specimens to F.Mueller, and published two papers of his own in *Proc. Roy. Soc. S. Australia*. His specimens are in MEL.

References: Hall, 1984; Roberts & Whitten, n.d.

Koch, Max

Born in Berlin, Germany, on 17 July 1854, died in Pemberton, Western Australia, on 1 April 1925.

Emigrated to Australia in 1878, and worked for many years (c. 1888–1901) on a sheep station at Mount Lyndhurst, South Australia. Moved to Western Australia in 1904, where he was employed in saw milling work. A prolific collector in his spare time, he amassed large numbers of collections from the mid-north of South Australia and from Western Australia. Ten sets of the Mount Lyndhurst specimens were sent to Maiden at NSW who used them as exchange with other herbaria. Seven sets from Mount Lyndhurst and 100 Western Australian plants were sent to AD. About 200–300 sheets of Western Australian collections were bought by MEL in about 1896. Audas (1929) credits him with discovering nine new species in South Australia, and 33 species plus 14 varieties from Western Australia. His main collections are at AD, MEL and NSW, with smaller sets at many herbaria including A, B, BP, BREM, BRI, CANB, DBN, E, G, GH, HBG, HO, K, L, M, MIN, MO, P, PERTH and VT. See Audas (1929) for an exhaustive list of institutions receiving specimens.

References: Audas, 1929; Hall, 1978; Nelson, 1980; Kraehenbuehl, 1986; Short, 1990b.

Portrait: Kraehenbuehl, 1986.

Collecting localities: Audas, 1929.

Labillardière, Jacques J.H. de

Born in Alençon, France, on 28 October 1755, died in Paris, France, on 8 January 1834.

Studied medicine and botany; travelled widely in Europe, including England, becoming a correspondent of Banks and J.E.Smith. In 1791–1794 he was botanist on the expedition commanded by Bruni d'Entrecasteaux (*Recherche* and *Espérance*) which visited Tasmania (Recherche Bay and D'Entrecasteaux Channel, 21 April–28 May 1792; Rocky Bay, D'Entrecasteaux Channel, Ralphs Bay, Frederick Henry Bay, Adventure Bay, 21 January–27 February 1793) and Esperance Bay, Recherche Archipelago (9–17 December 1792) in south-western Western Australia. In 1804–1807 he published *Novae Hollandiae Plantarum Specimen*, the most comprehensive account of the Australian flora to that time. It was based largely on his own collections, but included unacknowledged material from others, including Baudin (Nelson, 1975; Carr & Carr, 1976). His main herbarium is now at FI-Webb, with another extensive set at G. Occasional duplicates are in other herbaria, including B, BM, BR, C, CGE, CW, DBN, G, G-DC, GH, K, L, LINN, LIV, MEL, MO, NY, P, PH, P-JU, S, UPS, W, WELT.

References: Bailey, 1891; Maiden, 1910b; Stafleu, 1966a; Nelson, 1974, 1975; Carr & Carr, 1976; Apfelbaum, 1977; Hall, 1978; Carr & Carr, 1981a; Finney, 1984; Edmondson, 1993; Plomley & Piard-Bernier, 1993; Horner, 1995; Pearce, 1996.

Portraits: Maiden, 1910b; Carr & Carr, 1976, 1981a; Horner, 1995.

Maps of collecting sites: Nelson, 1975; Carr & Carr, 1976; Cohn & Almond, 1991; Plomley & Piard-Bernier, 1993; Horner, 1995; Pearce, 1996.

List of Tasmanian collections: Plomley & Piard-Bernier, 1993.

Lawrence, Robert W.

Born in England on 18 October 1807, died in Formosa, Tasmania, on 18 October 1833.

Arrived in Tasmania in April 1825. Recruited by W.Hooker in 1830 as a collector; forwarded specimens to Kew until 1832. Instrumental in recruiting Gunn as a collector for Kew. His main collection is in K, with some duplicates in G, MANCH, NSW and OXF.

References: Bailey, 1891; Maiden, 1909a; Hall, 1978; Buchanan, 1988b; Conn, 1994.

Lee, Alma T. (nee Melvaine)

Born near Tingha, New South Wales, in 1912, died in Sydney, New South Wales, on 20 October 1990.

During a long career, much of it with the National Herbarium of New South Wales, Alma Lee studied such diverse groups as soil algae, Fabaceae, *Lomandra*, *Psilotum, Tmesipteris, Typha* and *Xanthorrhoea*. Perhaps best known for her revisionary work in *Aenictophyton, Bossiaea, Crotalaria, Hovea, Lomandra*, *Lupinus, Platylobium, Psoralea, Swainsona, Templetonia, Typha* and *Xanthorrhoea*. The March 1991 issue of the journal *Telopea* was dedicated to her memory. Her collections are to be found in NSW.

Reference: Briggs, 1991.

Portrait: Briggs, 1991.

Leichhardt, F.W. Ludwig

Born in Trebatsch, Prussia, on 23 October 1813, died on an expedition in central Australia, 1848.

Well educated in natural history, Leichhardt arrived in Australia in February 1842. He led an expedition from Dalby (Queensland) overland to Port Essington (Northern Territory), October 1844–December 1845. A second expedition set out from the Darling Downs, Queensland, for Western Australia in 1846, but failed and returned. An attempt to repeat this expedition in 1848 resulted in the disappearance of the party without trace. Leichhardt was based in Sydney (New South Wales) between expeditions, and collected there, between Newcastle (New South Wales) and Moreton Bay (Queensland), and on his expeditions. His collections are lodged in MEL and NSW, with a few duplicates elsewhere (e.g. B, BM, HO and P).

References: Maiden, 1908a; Blake, 1954; Feeken *et al.*, 1970; Hall, 1978; Webster, 1980; Vallance, 1983; Robson, 1988; Barker & Barker, 1990; Jackes, 1990; Symons & Symons, 1997a.

Portraits: Feeken *et al.*, 1970; Webster, 1980; Gilbert, 1981; Jackes, 1990; Olde & Marriott, 1994.

Map of collecting localities: Blake, 1954.

Leschenault de la Tour, Jean B.L.T.

Born in Chalons-sur-Saone, France, on 13 November 1773, died in Paris, France, on 14 March 1826.

Botanist on the voyage of the *Géographe* and *Naturaliste* (Baudin, 1801–1803), which visited the north-west, west and south coasts of Western Australia, coastal South Australia, Port Jackson, New South Wales, and King Island in Bass Strait. Leschenault later visited Java, Cape Verde Islands, Cape of Good Hope, India, Sri Lanka, Brazil and British Guyana, but published little. His collections were subsequently used by other French botanists, including Bonpland, Desfontaines, de Jussieu, Labillardière and Ventenat. His herbarium was lodged in P, with some duplicates in FI, G-DC, G-DEL, H, K, L, MO, NY, OXF (150 specimens) and PC.

References: Bailey, 1891; Maiden, 1908c, 1910b, 1912; Osborn, 1952; Nelson, 1975; Carr & Carr, 1976; Diels (transl. Carr), 1981; Finney, 1984; Kraehenbuehl, 1986; Pearce, 1996, 1997.

Lesson, Rene P.

Born in Rochefort, France, on 20 March 1794, died in the same town on 28 April 1849.

Best known as a zoologist, but also skilled in botany, and professor of botany at Rochefort. Employed as a naturalist/collector on the *Astrolabe* in 1826–1829 (see Dumont d'Urville). His collections are mainly at P and PC, with some also in B, K, L and MO.

Reference: Maiden, 1910b.

Lhotsky, Johann

Born at L'vov, Ukraine, in 1795, died in London, England, in November 1866.

Collected in Brazil 1830–1832, before arriving in New South Wales in mid-1832. In 1834 he undertook a 3-month expedition to the Alps of New South Wales. From 14 October 1836 to 1 April 1838 he visited Tasmania, being engaged briefly by Governors Frankland and Franklin to collect specimens and carry out minor surveys around Hobart and the Tasman Peninsula. His herbarium was sold and dispersed. His Australian collections can be found, in part, at BM, with some in B, CN, FI, G-DEL, HAL, KIEL, LE, LY, LZ, MEL, OXF, P, W.

References: Maiden, 1908a; Kruta *et al.* 1977; Willis, 1977.

Lindley, John

Born in Catton, near Norwich, England, on 5 February 1799, and died in Turnham Green, Middlesex, England, on 1 November 1865.

Assistant librarian to Banks; Assistant Secretary to the Royal Horticultural Society (1822); first Professor of Botany at the University of London (1829–1860); lecturer in botany to the Apothecaries' Company (1836); later Professor of Botany at Cambridge University. It was on his Report to Treasury and Parliament that the Royal Garden at Kew was saved from destruction in 1838. One of Britain's foremost botanists, his particular connections with Australia included his descriptions of the plants of Mitchell's expeditions (1838) and an Appendix to the *Botanical Register* (1839) describing plants (mainly those of Drummond and Molloy) of the Swan River Colony, Western Australia. He was also instrumental in the appointment of Charles Moore as Director of the Sydney Botanic Gardens, New South Wales. His main herbarium (including collections sent from Australia) is in CGE, with some duplicates in BM and K (all orchids at K).

References: Maiden, 1909b; Stearn, 1965; Kruta *et al.*, 1977; Hall, 1978; Olde & Marriott, 1994.

MacGillivray, John

Born in Aberdeen, Scotland, on 18 December 1822, died in Sydney, New South Wales, on 6 June 1867.

Collected specimens in the Northern Territory and Queensland, at Port Essington, Raine Island and perhaps other localities along the Great Barrier Reef and Torres Strait during Bremer and Blackwood's Expedition in the *Fly*, 1838. Botanist on the voyages of *H.M.S. Rattlesnake* (Captain Owen Stanley, 1847–1850), collecting at Port Curtis, Rockingham Bay, Port Molle, Cape York, Gould Island, Lizard Island and Moreton Islands in Queensland, Port Essington (Northern Territory) and visiting Sydney (New South Wales) on several occasions. The expedition was in Hobart, Tasmania, in June 1847 and also surveyed in Bass Strait, and on the southern coast of New Guinea and the Louisiade Archipelago. He was a member of expeditions to the Fly and Bramble Rivers in 1842–1846, and on the voyage of the *Herald* (1852–1861). On the latter expedition, which visited, *inter alia*, Lord Howe Island, New South Wales, Dirk Hartog Island and Shark Bay, Western Australia, he was accompanied by William Milne (?–1866). His herbarium is mainly in BM and K, with some duplicates in B, BO, E, G-DC, L, LA, MEL, MO, NY, P and W.

References: Bailey, 1891; Maiden, 1910a; Calaby, 1967; Gilbert, 1981; Olde & Marriott, 1994.

Portrait: Maiden, 1910a.

Maconochie, John R.

Born in Adelaide, South Australia, on 13 June 1941, died in a road accident in Somalia, 24 January 1984.

Botanist in charge of the Alice Springs Herbarium (NT) from 1967 until 1984. His research interests were mainly in ecology, but he contributed to the taxonomy of *Cycas, Hakea* and other Northern Territory plants. His Australian herbarium at NT was largely transferred to DNA. Collections from Oman are in ON.

Reference: Hall, 1984.

Maiden, Joseph H.

Born in St John's Wood, London, England, on 25 April 1859, died in Turramurra, New South Wales, on 16 November 1925.

Arrived in New South Wales in 1880. First curator of the Technological Museum, Sydney (1881–1896), where he established an herbarium from 1883; consulting botanist to the Department of Agriculture from 1890; Superintendent of Technical Education from 1894. Appointed Government Botanist and Director of the Botanic Gardens in Sydney in 1896, retiring in 1924. He was instrumental in establishing the formal herbarium, with a purpose-built building, a botanical museum and lecture room, and established a network of collectors and correspondents. He collected widely in Western Australia, South Australia, New South Wales, Victoria and on Lord Howe, Norfolk and Pitcairn Islands. His research output was prodigious, including the 8-volume *A Critical Revision of the Genus Eucalyptus* (1903–1933), the 8-volume *Forest Flora of New South Wales* (1903–1925), several major papers on *Acacia*, and (with E.Betche) *A Census of New South Wales Plants* (1917). He wrote a series of papers from 1908–1921 giving biographical details of early Australian botanists, and these papers have been heavily used in subsequent histories, including this one. His main collection is in NSW, with duplicates in many other herbaria, including A, AK, B, BISH, BM, C, CGE, CORD, DAO, DBN, E, F, GB, GH, HBG, HO, K, L, LIV, MANCH, MICH, MO, MSE, NH, NY, OXF, POM, U, VT, W and WAG.

References: Froggatt, 1932; Blake, 1954; Hall, 1978; Nelson, 1980; Gilbert, 1981; Edmondson, 1983; Gilbert, 1986; Olde & Marriott, 1994.

Portraits: Hall, 1978; Gilbert, 1981, 1986.

Mangles, James

Born in England in 1786, died in Fairfield, Exeter, England, on 18 November 1867.

As a naval Captain he visited the Swan River Colony (Western Australia) in 1831. On his return to England he commissioned James Drummond (through George Fletcher Moore) to collect seeds, plants and herbarium specimens which he sold to nurserymen (particularly C.Loddiges). He also received seeds and plants from Georgiana Molloy. He and his brother Robert were connected to the shipping company F. & C.F.Mangles, which inaugurated a regular service to the colony from 1835. His herbarium is in B, CGE and GH.

References: Maiden, 1909b; Erickson, 1969; Hall, 1984; Lines, 1994; Olde & Marriott, 1994; Pearce, 1996.

Maxwell, George

Born in England in April 1804, died at Middleton Beach, Albany, Western Australia, in January 1880.

By 1846 he was established in Albany, where he made at least a partial living as a professional collector of natural history items. He accompanied Drummond to the Stirling Range, Western Australia (1846–1847) and also accompanied Mueller on a number of long journeys. His main collection is in MEL, with substantial numbers also in BM and K. Some are also in B, CANB, KIEL, MANCH, M, PERTH and W.

References: Maiden, 1909b, 1912; Hall, 1978; Olde & Marriott, 1994.

Menzies, Archibald

Born in Weem, Perthshire, Scotland, on 15 March 1754, died in Notting Hill, England, on 15 February 1842.

Accompanied Captain Vancouver on his round-the-world voyage (1791–1795) in *Discovery*, on the recommendation of Banks. Vancouver explored the West Australian coastline from Cape Chatham [Chatham Island] to about the middle of the Great Australian Bight, discovering and anchoring at King George Sound for two weeks in 1791. Here Menzies made a large number of dried and living collections, particularly Proteaceae. The ship also touched at Doubtful and Termination Islands in the Recherche Archipelago. Specimens were forwarded to Banks from Sydney, others returned with the ship in 1796. Seed from King George Sound was raised at Kew. His Australian herbarium is now lodged at BM and K. Smaller numbers of specimens are also at CGE, LINN, LIV, MANCH, MO, OXF and P.

References: Bailey, 1891; Maiden, 1909b; Nelson, 1975; Finney, 1984; Hall, 1984; Barker & Barker, 1990; George, 1991; Edmondson, 1993.

Milligan, Joseph

Born in Dumfries, Scotland, in 1807, died in London, England, in 1884.

A surgeon with the Van Diemen's Land Company at Hampshire Hills/Surrey Hills grazing block in north-western Tasmania, 1831–1842; joined Governor Sir John & Lady Franklin's overland expedition to Macquarie Harbour (February–May 1842); later stationed at Flinders Island (December 1843–April 1846 and May–October 1847) and Macquarie Harbour (July 1846–March 1847). He collected on the east coast of Tasmania (Schouten Island, Recherche Bay and Fingal) in 1848, and in the east and north from 1849–1854. An acquaintance of James Backhouse in the 1830s, and later a member of Gunn's collecting circle (1840s and 1850s). Secretary of the Royal Society of Van Diemen's Land, 1848–1860. He presented a collection of flowering plants to the Tasmanian Museum in 1852, before leaving Tasmania in 1860. Many of his collections were incorporated in Gunn's herbarium, and thus are now found in BM, HO, K and NSW. Some are also recorded in A, CGE, F, FI, MEL, MO, OXF, P and TCD.

References: Maiden, 1909a; Osborn, 1952; Burns & Skemp, 1961; Lander, 1988b; Buchanan, 1988b, 1990.

Portrait: Buchanan, 1988b.

Map of collecting localities: Buchanan, 1988b.

Miquel, Friedrich A.W.

Born in Neuenhaus, Bentheim, Germany, on 24 October 1811, died in Utrecht, Netherlands, on 23 January 1871.

A Dutch botanist who never visited Australia, but accumulated a large private herbarium through a network of correspondents. He wrote on several important Australian families, and described a number of Australian species, particularly in the cycads, Casuarinaceae, Myrtaceae, Piperaceae and Polygonaceae. His main herbarium is now in U, but some of his Types can be found in G, K, L, MEL and P.

References: Maiden, 1908a; Stafleu, 1966b, 1974; Hall, 1978.

Portrait: Stafleu, 1974.

Mitchell, Sir Thomas L.

Born in Stirlingshire, Scotland, on 15 June 1792, died in Darling Point, New South Wales, on 5 October 1855.

After a military career, Mitchell arrived in Sydney, New South Wales, in 1827 to take up the position of Deputy Surveyor-General. On Oxley's death in 1828 he became Surveyor-General, and held the position until 1855. He led four major expeditions, to north-western New South Wales in 1831, to Bourke and down the Darling River in 1835, along the Lachlan River to the Murrumbidgee and Murray Rivers and into western, central and north-eastern Victoria in 1836, and to mid-western Queensland in 1845–1847. Botanists accompanied him in 1835 (Richard Cunningham, killed early in the expedition), 1836 (John Richardson) and 1845–1847 (William Stephenson). The first three expeditions were described in *Three Expeditions into the Interior of Eastern Australia* (1838), in which John Lindley described 77 new species of plants. Mitchell's collections are at BM (specimens sent to Brown, and others donated later by Mitchell), CGE (those sent to Lindley) and K (specimens sent to W.Hooker). A few are also at E, GH, L, MEL, NSW, TCD and W. Mitchell also presented a collection to the Australian Museum, later transferred to the Sydney Botanic Gardens, New South Wales, and rediscovered in a dilapidated state in 1896 (Gilbert, 1986).

References: Bailey, 1891; Maiden, 1908a; J.Willis, 1949a; Hall, 1978; Barker & Barker, 1990; Cohn & Almond, 1991; Willis & Cohn, 1993.

Portraits: Feeken *et al.*, 1970; Willis & Cohn, 1993.

Molloy, Georgiana

Born in Carlisle, Cumberland, England, on 23 May 1805, died at 'Fairlawn', near Busselton, Western Australia, on 8 April 1843.

Arrived in Western Australia in March 1830. In 1836 she was invited to collect seeds and plants by James Mangles, and these were used to establish many Australian plants in cultivation in England. Her specimens were described by Lindley, and later by other botanists including W.Hooker and Meissner. Her collections are at B, CGE and K.

References: Erickson, 1969; Bassett, 1981; Moyal, 1981; Hall, 1984; Lines, 1994.

Portrait: Lines, 1994.

Moore, Charles

Born in Dundee, Scotland, on 10 May 1820, died in Sydney, New South Wales, on 30 April 1905.

Arrived in Sydney on 14 January 1848 to take up the position of Director, Botanic Gardens, Sydney, a position he occupied until 5 May 1896. He undertook numerous collecting expeditions in eastern New South Wales, and from 1850 delivered lectures in botany to medical students and others. In 1850 he collected in the New Hebrides [Vanuatu], Queen Charlotte Group, Solomon Islands and New Caledonia. Moore visited Lord Howe Island in 1869, and published a report on the vegetation (1870). He wrote a census of New South Wales plants (1884) and (with E.Betche) a *Handbook of the Flora of New South Wales* in 1893. His main collections are in K, with others in BM, E, FI, MEL and NSW. Moore sent collections to Mueller at first, but later, after a disagreement with him, forwarded at least some directly to Bentham (Green, 1989).

References: Maiden, 1908a; Froggatt, 1932; Hall, 1978; Gilbert, 1981, 1986; Green, 1989; Olde & Marriott, 1994.

Portraits: Gilbert, 1981, 1986.

Moore, Spencer le M.

Born in Hampstead, London, England, on 1 November 1850, died in mid-March 1932.

Undertook an expedition in Western Australia from the Goldfields region in December 1894–October 1895, travelling from Southern Cross to Siberia Soak, Goongarrie, Menzies, Mt Margaret, Bates Range, Lake Darlot and Coolgardie. His collections are at B, BM, K, MEL, MO and NY.

References: Hall, 1978; Diels (transl. Carr), 1981; Olde & Marriott, 1994.

Moore, Thomas B.

Born in New Norfolk, Tasmania, on 26 November 1850, died in Queenstown, Tasmania, on 14 August 1919.

Surveyor and prospector in western Tasmania from 1868; visited Temora, New South Wales (1880), Victoria (1882–1883) and Sydney and Brisbane (1885). Sent specimens to Rodway. His bryophyte collections in HO, from the west coast of Tasmania, date from 1897 to 1907. The R.G.Brett *Eucalyptus* collection in HO (duplicates in MEL) apparently passed through his hands.

Reference: Hall, 1978.

Morris, Albert

Born in Bridgetown, South Australia, on 13 August 1886, died in Broken Hill, New South Wales, on 9 January 1939.

Made a collection of about 8000 specimens from Broken Hill and western New South Wales, which was donated to the Waite Institute in South Australia. This herbarium was transferred to AD in 1985. A few specimens are also in A, K, NSW, NY and WELC.

References: Hall, 1984; Kraehenbuehl, 1986.

Morris, Dennis I.

Born near Tunbridge Wells, England, on 16 May 1924.

Came to Australia in 1950. Morris joined the Tasmanian Department of Agriculture, serving as Technical Officer, particularly concerned with weeds, and published a number of handbooks and papers on both the native and naturalised flora. He was a part-time lecturer in the Agricultural Science Department of the University of Tasmania for several years. In 1970 he began a continuing collaboration with Winifred Curtis on the final parts of her *Students' Flora of Tasmania*. He retired in 1985, but continues as an Honorary Botanist at the Tasmanian Herbarium. His main herbarium is in HO, with duplicates in many other herbaria, including BRI, K, MEL and NSW.

References: Hall, 1984; Curtis & Morris, 1994.

Morrison, Alexander

Born in Wester Dalmeny, near Edinburgh, Scotland, on 15 March 1849, died in Cheltenham, Victoria, on 7 December 1913.

Morrison was a retired medical practitioner in 1897 when he was appointed as Western Australia's first official botanist in the Bureau of Agriculture. He was retrenched from this position in 1906, again becoming a practicing doctor before moving to Melbourne in 1912. Here he was associated with Ewart at MEL in the year before his death. He collected extensively in Western Australia and Victoria, briefly at Gawler in South Australia, and undertook an excursion to the New Hebrides (Vanuatu) in 1896. Morrison amassed a sizeable private herbarium, which he bequeathed to the University of Edinburgh. Of these, E now holds about 9000 specimens, about 5000 were donated to K in 1930, and about 7000 were distributed to AD, CANB, MICH, PERTH and US. Other herbaria known to have some specimens are A, B, BM, BRI, CORD, GH, L, MEL, MO, NH, NSW, P, S, US, WAG and WRSL.

References: Maiden, 1921; Hall, 1978; Green, 1990; Lamond & Bennell, 1990; Olde & Marriott, 1994.

Portrait: Lamond & Bennell, 1990.

List of collecting localities: Lamond & Bennell, 1990.

Mueller, Ferdinand J.H. von

Born in Rostock, Germany, on 30 June 1825, died in Melbourne, Victoria, on 10 October 1896.

A trained pharmacist and botanist, Mueller arrived in Adelaide, South Australia, on 15 December 1847, and began collecting immediately. From 1847 until 1853 he collected around Adelaide, the Barossa Valley, and the Murray Scrub. In 1847 (and later in 1876) he collected in the South East, and in 1851 explored the Flinders Ranges as far north as Wilpena Pound. Mueller moved to Melbourne, in August 1852 and was almost immediately appointed first Government Botanist for Victoria, a position he held from 28 January 1853 until his death. In his first three years in the post he undertook three major expeditions, totalling perhaps 9000 km, visiting most regions of the colony, and crossed into New South Wales to Mt Kosciuszko. He joined Gregory's North Australian Exploring Expedition (1855–1857), being given the additional responsibility of Director of the Botanic Gardens on his return. He was Director from 1857 until 1873. Mueller undertook many shorter collecting trips during his subsequent career (see Churchill *et al.* 1978 for summary), and built up an extensive network of correspondents and collectors throughout the country. The Melbourne Herbarium was the focus of Australian taxonomic work throughout the last half of the 19th century, and remains the largest single collection in the country, and the one with the highest numbers of historically important collections. Mueller was, in addition to his collecting activities, a prodigious writer, and produced over 1000 papers and books. He described over 2000 new species, many in *Fragmenta Phytographiae Australiae*, published in 94 fascicles between 1858 and 1882. He wrote two censuses of Australian vascular plants (1882, 1889) but was unable to achieve his dream of writing an Australian Flora. Instead he sent the contents of the Melbourne Herbarium to Bentham in consignments over 16 years, resulting in the latter's *Flora Australiensis* (1863–1878). In later life Mueller was an early and strong campaigner for conservation of Australia's native plants and animals. The personal herbarium and library of Mueller became the property of the Government of Victoria on his death, and are now housed in MEL. Duplicates of his collections are found in many herbaria around the world, including AK, BM, CAL, CANB, DBN, GH, GRA, K, M, NSW, P, TCD and W.

References: Bailey, 1891; Maiden, 1909b; J.Willis, 1949a; M.Willis, 1949; Churchill *et al*., 1978; Muir, 1979; Kynaston, 1981; Forbes, 1983; Kraehenbuehl, 1983b; Vallance, 1983; Churchill *et al*., 1984; Kraehenbuehl, 1986; Womersley & Sinkora, 1987; Cohn, 1989; Grandison, 1990b; Cohn & Almond, 1991; Maroske *et al*., 1991; Gillbank, 1992; Maroske & Cohn, 1992; Willis & Cohn, 1993; Olde & Marriott, 1994; Ross, 1995; Maroske, 1996; Taylor, 1996; Dwyer, 1996a, 1996b; Houghton, 1996; May & Maroske, 1996; Ross, 1996.

Portraits: M.Willis, 1949; Churchill *et al*., 1978; Kynaston, 1981; Gilbert, 1985; Kraehenbuehl, 1986; Maroske *et al*., 1991; Willis & Cohn, 1993; Olde & Marriott, 1994.

Maps of itineraries: Cohn & Almond, 1991; Albrecht, 1996; Grandison, 1996; Parkin, 1996a.

Née, Luis

Born in France but worked most of his life in or for Spain.

With Fadeo (Thaddeus) Haenke he visited Port Jackson, New South Wales, in 1793 as botanist on the Alejandro Malaspina expedition (*Descubierta* and *Atrevida*), collecting more than 1000 specimens, many of which were described by Antonio José Cavanilles in 1797–1800 (*q.v.*). His collections are at MA, with duplicates in B, C, DS, F, FI, KIEL, MPU and NY.

References: Hall, 1978; Gilbert, 1981.

Nelson, David

Date of birth unknown, died in Kupang, Timor, on 20 June 1789.

Gardener at Kew, who accompanied William Anderson (Surgeon) on the *Resolution* (Cook's third voyage) as official plant collector, sponsored by Banks. He collected at Adventure Bay, Bruny Island, Tasmania, 26–30 January 1777, his specimens including the Type of *Eucalyptus obliqua*, on which the genus was based. In 1787 he was botanical collector on the *Bounty*, which called at Adventure Bay, and was with Bligh on his epic open boat voyage after the mutiny, dying of exposure and fever after arrival at Timor. His main collection is at BM, with a few duplicates in E and HO.

References: Bailey, 1891; Maiden, 1909a, 1921; Hall, 1978; Finney, 1984.

Newbey, Kenneth R.

Born in Katanning, Western Australia, on 11 June 1936, died in White Gum Valley, Western Australia, on 24 July 1988.

A plant ecologist and collector, particularly active in the Albany–Esperance area, southern wheatbelt, goldfields and the Pilbara of Western Australia. His main herbarium of about 12 000 specimens is in PERTH, with other collections in the regional herbaria at Albany and Karratha, Western Australia.

References: Hall, 1984; Maslin, 1988b; Newbey & Maslin, 1990; Hall, 1993; Olde & Marriott, 1994.

Portrait: Newbey & Maslin, 1990.

Nicholls, William H.

Born in Ballarat, Victoria, on 23 July 1885, died in Footscray, Victoria, on 10 March 1951.

An amateur botanist, he was one of the first to study orchids in Australia. He published over 150 articles in Victorian and Queensland naturalist journals, and was an accomplished watercolourist. His paintings were published posthumously as *Orchids of Australia* (1951–1958, 1969). His collection of over 5000 specimens is now in MEL.

References: J.Willis, 1949b, 1951, 1988b; Cohn & Almond, 1991; Willis & Cohn, 1993.

Portrait: Willis, 1951.

Oldfield, Augustus F.

Born in London, England, on 12 January 1821, and died there on 22 May 1887.

Collected in Tasmania, probably in about 1858, particularly in the Huon Valley and on the mountains. Visited Twofold Bay in New South Wales. Walked from Sydney to Melbourne in the late 1840s. Major collections were made in Western Australia in the coastal strip from Murchison River to King George Sound, and across the Nullarbor Plain towards Adelaide. His main herbarium is now in MEL, sent by him to Mueller. Substantial numbers of specimens are also in K, donated by his brother after his death, and in W. A few duplicates are in B, BR, CANB, CGE, E, MANCH, OXF, S, SAM and US.

References: Maiden, 1909a, 1909b, 1912; Hall, 1978; Olde & Marriott, 1994.

Orchard, Anthony (Tony) E.

Born in North Adelaide, South Australia, 22 May 1946.

Botanist, State Herbarium of South Australia (AD) (1972); Curator, Cheeseman Herbarium (AK) (1972–1978); foundation Curator, Tasmanian Herbarium (HO) (1978–1992); Editor/Executive Editor, *Flora of Australia* (1992–1998), Director, ABRS Flora Section (1998–). Main research interests in Rosaceae, Haloragaceae, Asteraceae, Rubiaceae. Collections mainly in AD (pre-1972), AK (New Zealand, some Australia) and HO (Tasmania), but duplicates widely distributed.

Reference: *Pers. comm.*

O'Shanesy, Patrick A.

Born in Ratto, Ireland, in 1837, died in Rockhampton, Queensland, in December 1884.

Arrived in Brisbane, Queensland, in 1864 to join his brother John O'Shanesy (1834–1899, see Hall, 1984) in a nursery/orchard business in Rockhampton (1864–1870) and Kabra (1870–). The two brothers (but particularly Patrick) were regular correspondents of F.Mueller, and collected widely in the Rockhampton district. Their collections are in MEL.

References: Maiden, 1910a; Hall, 1978.

Map of collecting localities: Blake, 1954.

Ostenfeld, Carl E.H.

Born in Randers, Denmark, on 3 August 1873, died in Copenhagen, Denmark, on 16 January 1931.

Visited Western Australia from 18 August to 7 November 1914, collecting mainly in near-coastal localities between Albany and Derby. He was also given collections made by Western Australian residents, including C.Andrews, Miss G.Davis, Mrs M.Davis, E.Dorph-Petersen, E.Douglas, Mrs Hardman, Dr Lessing and O.H.Sargent. His main Australian herbarium of about 1300 numbers is in C, with duplicates in B, CANB (c. 75), DBN (c. 670), K (80), MEL and PERTH.

References: Nelson & Scannell, 1978; Nelson, 1980; Smith, 1985; Kenneally *et al.*, 1996.

Map and list of collecting localities: Nelson & Scannell, 1978.

Paterson, William

Born in Montrose, Scotland, on 10 August 1755, died at sea on 21 June 1810.

Trained in horticulture, later obtaining a commission in the 98th Regiment (1781–1785), 102nd Regiment (Captain) and the New South Wales Corps (Lieutenant-Colonel, 1789). Collected in southern Africa, India and later in Australia. Commander of the detachment on Norfolk Island (1791–1793) producing a manuscript account of the plants of Norfolk Island which was sent to Banks, but remained unpublished. First commandant (Lieutenant Governor) of the northern settlement (Port Dalrymple) in Tasmania (1804), and Lieutenant Governor of New South Wales (1800–1810). Sent pressed specimens to Banks, and seeds to several British nurserymen. His herbarium is at BM, with a few duplicates at CGE, DBN, E, G and HO.

References: Bailey, 1891; Nelson, 1980; Finney, 1984; Hall, 1984; Barker & Barker, 1990; Olde & Marriott, 1994; Nelson, 1996.

Pérouse, Jean-François de G. de la

Born near Albi, France, on 23 August 1741, died at Vanikoro Island, Santa Cruz, in 1788.

Commander of an expedition to the South Seas in the ships *Boussole* and *Astrolabe* which called into Port Jackson, New South Wales, a few days after the arrival of the First Fleet (1788). Shortly afterwards both vessels were wrecked on Vanikoro Island in the Santa Cruz group, the wreckage being discovered by the English Commander Peter Dillon in 1828. Their loss triggered subsequent, more successful voyages carrying French naturalists such as Gaudichaud, Labillardière, Leschenault and Dumont d'Urville.

Reference: Finney, 1984.

Portrait: Horner, 1995.

Phillips, E. Marie

Born in Melbourne, Victoria, in 1917, died in Goulburn, New South Wales, in 1977.

Appointed Botanist at the Canberra Botanic Gardens (now Australian National Botanic Gardens), Australian Capital Territory, in June 1960, succeeding Erwin Gauba. She was largely responsible for a major acceleration in the development of the herbarium (CBG) and for devising a rigorous cross-referencing system tying the living collections to vouchers in the herbarium. She collected widely, both for living collections and herbarium purposes, in southern, eastern and western Australia. She retired in December 1973. Her collections were lodged in CBG, now transferred to CANB.

References: Court, 1980; Wrigley, 1980; Olde & Marriott, 1994.

Preiss, J.A. Ludwig

Born in Herzberg am Harz, Germany, on 21 November 1811, and died there on 21 May 1883.

Visited the Swan River colony, Western Australia, from December 1838 to January 1842, making a collection of about 3000–4000 specimens from an area extending from about 100 km north of Perth south to Albany and east to the vicinity of Cape Riche. These collections (with a few by other collectors) form the basis for one of the landmark works on Western Australian botany, *Plantae Preissianae...* (Lehmann, 1844–1848). Preiss' collections were made up into various sets and subsequently dispersed, now being found in at least 25 different herbaria. The standard reference set for *Plantae Preissianae* is now at LD (Crisp, 1983), with other substantial numbers of specimens at C, DBN, G, HBG, LE, MEL, MO, P, S and W. For minor holdings in other herbaria see McGillivray (1975), Nelson (1981a), Lander (1988) and Maslin & Cowan (1994b). The MEL collections were purchased as part of the Steetz and Sonder herbaria.

References: Bailey, 1891; Maiden, 1909b; McGillivray, 1975; Hall, 1978; Nordenstam, 1980; Nelson, 1981a; Crisp, 1983; Wilson, 1983; Hilton, 1988; Lander, 1988; Short & Sinkora, 1988; Short, 1990b; Marchant, 1990b; Cohn & Almond, 1991; Maslin & Cowan, 1994b; Olde & Marriott, 1994.

Pritzel, Ernst G.

Born in Germany on 15 May 1875, died, probably in Berlin, Germany, on 6 April 1946.

Accompanied Diels (*q.v.*) on his collecting expedition to Australia in 1900–1902. Some of his collections remain in B, others can be found in A, AD, B, BM, BR, C, DBN, E, F, GH, HBG, K, L, LAU, M, MEL, MICH, MO, NSW, NY, P, PERTH, PH, PR, S, US, VT, W, WRSL, Z.

References: Hall, 1978; Diels (transl. Carr), 1981; Short, 1990c.

Pryor, Lindsay D.

Born in Moonta, South Australia, on 26 October 1915, died in Canberra, Australian Capital Territory, on 17 August 1998.

Trained as a forester in South Australia and the Australian Capital Territory; Director of Parks & Gardens, Australian Capital Territory (1944–1958); first Professor of Botany, School of General Studies, Australian National University, Australian Capital Territory (1958–1976). Undertook work on the breeding and genetics of *Eucalyptus*, and in 1971 published (with L.A.S.Johnson), *A Classification of the Eucalypts*, which provided the first complete overview of the genus since Blakely. While Director of Parks & Gardens, Australian Capital Territory, he was primarily responsible for the initial planning and development of the Canberra Botanic Gardens (now Australian National Botanic Gardens). Under his direction the foundations of an herbarium were laid by Erwin Gauba. His collections are housed at GAUBA, with some in CANB.

References: Hall, 1978; Court, 1980; Wrigley, 1980.

Reader, Felix M.

Born in Berlin, Germany, in 1850, died in Dimboola, Victoria, on 24 March 1911.

A pharmacist, with a business in Dimboola, in the 1890s and early 1900s, and prolific collector of phanerogams and cryptogams, particularly of the Wimmera. Apparently collected in south-eastern South Australia in 1908. Published extensively in *Victorian Naturalist* (mosses described by V.Brotherus and C.Müller). His collection of about 10 000 specimens was purchased by MEL in 1906 for £80. Duplicates are in A, B, E, G, H, JE, K, L, MO, NH, NY, P and WAG.

References: Maiden, 1921; J.Willis, 1949b, 1949c; Kraehenbeuhl, 1983c; Hall, 1984; Short, 1990b; Short, 1990c.

Richards, Annie F. & Thomas, P.

Thomas Richards: born in England, 1842, died 1915. Annie Richards: details not known.

Thomas Richards was resident constable at Streaky Bay on Eyre Peninsula, South Australia, in the late 19th century. He was guide to Giles 4th Expedition between Fowlers Bay and Ooldea. He and his wife Annie sent extensive collections from Eyre Peninsula (especially the north-west), the mid-north, and from the northern Mount Lofty/southern Flinders Range area to Mueller between 1873 and 1894. These collections are now in MEL.

References: Hall, 1978; Kraehenbuehl, 1986.

Richardson, John M.

Born in England c. 1797, died in Newcastle, New South Wales, on 28 July 1882.

Transported to Hobart, Tasmania, in 1822; shortly afterwards employed as a gardener at Sydney Botanic Gardens, New South Wales. A member of Oxley's 1823 and 1824 expeditions, he moved to Melville Island (Northern Territory) 1826–1828, collecting also on Timor (1826). In 1836 he was collector on Mitchell's expedition, and also collected in New South Wales in later life. His collections are probably in BM, CGE or K.

References: Maiden, 1908a; Hall, 1984.

Riche, Claude A.G.

Born in Chamelet en Beaujolais, France, on 20 August 1762, died in Mont d'Or, France, on 5 September 1797.

Naturalist (principally an entomologist) on the *Espérance*, commanded by Bruni d'Entrecasteaux, which visited Western Australia and Tasmania in 1791–1794. His botanical collections were probably subsumed into those of Labillardière (*q.v.*).

References: Maiden, 1910b; Plomley & Piard-Bernier, 1993; Pearce, 1996.

Robertson, Enid L.

Born 1925.

Appointed to the Waite Institute, South Australia, as Systematic Botanist in 1947, replacing Con Eardley as curator of the ADW herbarium. From 1953–1955, Senior Research Fellow at the Botany Department, University of Adelaide. She has published on Asteraceae, *Danthonia* and seagrasses, and revised Part 4 of J.M.Black's *Flora of South Australia* (2nd edn). Her herbarium was lodged at ADW, now transferred to AD.

Reference: Gardner, 1990.

Portrait: Gardner, 1990.

Robertson, John G.

Born in Glasgow, Scotland, on 15 October 1803, died at 'Baronald' near Lanark, Scotland, in 1862.

Collected in India in 1828 before emigrating to Tasmania in 1831. Manager of Lawrence's estate 'Formosa'. Collected in Tasmania and Victoria, with the encouragement of Gunn. Moved to Victoria in 1840–1841. Collected extensively on his property 'Wando Vale' near Casterton, Victoria, from at least January 1842–May 1844, and in the south-east of South Australia. His Tasmanian collections were forwarded to Gunn, and thus are mainly at K, with some at E, HO and MEL. He returned to England in the mid-1850s with a personal collection of 4000 Victorian specimens which he donated to W.Hooker, and these are also in K. A few specimens are also in MEL.

References: Willis, 1949c; Kraehenbuehl, 1983b, 1986; Buchanan, 1988b; Willis & Cohn, 1993; Roberts & Whitten, n.d.

Rodway, Frederick A.

Born in Hobart, Tasmania, on 25 March 1880, died in Nowra, New South Wales, on 1 April 1956.

Son of Leonard Rodway (*q.v.*). Collected in New South Wales (South Coast, based at Nowra) and Western Australia. He donated his herbarium of 15 000 specimens to NSW in 1952. Some of his Western Australian specimens are in HO (presumably sent to his father). The New South Wales collections are housed at NSW, some being collected by his daughter Gwenda Rodway (later G.Davis, NE, noted for early work on embryology of Australian plants). Duplicates are mainly at K, with a few in A, BISH, DAO and MO.

Reference: Anonymous, 1952; *pers. comm.* June Hewer (granddaughter of L.Rodway), per Ann Elias; *pers. comm.* Margaret Chambers (granddaughter of F.Rodway), per Karen Wilson; Olde & Marriott, 1994.

Rodway, Leonard R.

Born in Torquay, England, on 5 October 1853, died in Kingston, Tasmania, on 9 March 1936.

Arrived in Tasmania (via Queensland) in 1880 and practised as a dentist. Appointed Honorary Dental Surgeon at Hobart General Hospital (1890–1922). Appointed Honorary Government Botanist in 1896, and held the position until 1932. In 1928 he was appointed Honorary Curator of the Tasmanian Museum Herbarium, until his resignation in 1932. He was lecturer in botany at the University of Tasmania (1923–1929) and a trustee of the Tasmanian Museum and Botanic Gardens (1911–1923). For 30 years he was the premier authority on the Tasmanian flora, and gathered a group of correspondents and collectors to build the herbarium. Many of these were family members, including Olive Rodway, his second wife; Frederick and Ernest Rodway, his sons; John Rodway, his grandson (son of Ernest); Gwenda Rodway (later G.Davis), his granddaughter (daughter of Frederick); and C.L.Rodway (relationship unknown). Rodway published extensively on the Tasmanian flora, with his major work being *The Tasmanian Flora* (1903). He also published a series of major monographs in the *Papers & Proceedings of the Royal Society of Tasmania* on bryophytes (1912–1916) and numerous papers on fungi (1897–1930). His herbarium is housed in HO, with duplicates in A, AK, B, CANB, H, K, MEL, NSW and PRE.

References: Anonymous, 1936; Anonymous, 1950a; Anonymous, 1951; Hall, 1978; Elias, 1988.

Roe, John S.

Born in Newbury, Berkshire, England, on 8 May 1797, died in Western Australia on 28 May 1878.

First Surveyor-General of Western Australia. He undertook 16 expeditions in Western Australia, primarily in search of pastoral country. On his expeditions he also collected mineral, plant and animal specimens. The plant specimens were sent to K, with some also in G. He was instrumental in training later explorers, particularly Forrest (*q.v.*) and the Gregory brothers (see A.C.Gregory).

References: Maiden, 1909b; Feeken *et al*., 1970; Hall, 1978; Olde & Marriott, 1994.

Portrait: Feeken *et al*., 1970.

Rogers, Richard S.

Born in Adelaide, South Australia, in 1862, and died there on 28 March 1942.

A physician with wide-ranging interests, including forensic medicine and mental diseases. A student of Tate and colleague of Mueller, Rogers developed an early interest in orchids, going on to describe 66 new species, and publishing a handbook on the subject in 1911. He collected mainly in South Australia, but had at least one collecting trip to Victoria. His herbarium is now at AD, with duplicates in BM, G and MEL.

References: Hall, 1978; Kraehenbuehl, 1983c, 1986.

Portrait: Kraehenbuehl, 1986.

Royce, Robert D.

Born in Perth, Western Australia, on 14 March 1914.

Curator of the Western Australian Herbarium 1960–1974, having worked in the Department of Agriculture since 1937. He oversaw the planning and construction of the present herbarium building. His main research interests were in floristics and toxic plants. His substantial collection is lodged at PERTH, with duplicates in B and CANB.

References: Hall, 1978; Olde & Marriott, 1994.

Rupp, Hermann M.R.

Born in Port Fairy, Victoria, on 27 December 1872, died in Sydney, New South Wales, on 2 September 1956.

An Anglican Minister stationed for much of his working life in New South Wales country districts, but spending a few years in Tasmania (1920–1922), and visiting Victoria on a number of occasions. Rupp collected widely in most plant groups, although in later life he is best known for his collections and studies of orchids. The major part of his herbarium is now housed in the Botany School, University of Melbourne (MELU), with another large collection at NSW (presented 1946), and smaller collections elsewhere, including A, AK, DAO, DPU, G, HO, K, MEL, MO and W.

References: Hall, 1984; I.Clarke, 1990.

Portrait: I.Clarke, 1990.

Map of collecting localities: I.Clarke, 1990.

Sargent, Oswald H.

Born in Selley Oak, near Birmingham, England, on 5 December 1880, died in York, Western Australia, on 4 March 1952.

Emigrated with his family to Western Australia in 1886, living for most of his life at York, where he and his father were pharmacists. Best known for his studies of orchids, on which he published a large number of papers. His herbarium was donated to PERTH in 1928.

Reference: Hall, 1978.

Schomburgk, Richard M.

Born in Freyburg, Germany, in 1811, died in Adelaide, South Australia, in 1891.

Trained as a gardener in Germany, he joined his brother Robert on a joint British/Prussian scientific expedition to British Guyana in 1844. He emigrated to South Australia in 1849, settling with other family members near Gawler. Appointed Director of the Adelaide Botanic Garden in 1865, developing much of its present infrastructure (Palm House, tropical house for *Victoria amazonica*, Museum of Economic Botany, etc.) over the next 25 years. He was influential in encouraging street tree plantings in Adelaide, and in early forest conservation measures, and established the major plantings in Adelaide's Botanic Park. Under his directorship numerous potential crop plants were trialled, particularly forage and pasture species. He developed the first institutional herbarium and botanical library in Adelaide. He made few botanical collections, but his world-wide reference collection is now at AD.

Reference: Payne, 1988.

Schultz, M.

Dates of birth and death unknown.

Collected a large number of specimens in the early years of the Port Darwin settlement, Northern Territory. These were forwarded by Richard Schomburgk to K, where they were used by Bentham in *Flora Australiensis*.

References: Bailey, 1891; Maiden, 1908c; Hall, 1984.

Schwarz, Otto K.A.

Born in Thuringia, Germany, on 28 April 1900, died, probably in Jena, Germany, on 7 April 1983.

Studied in Jena 1919–1920, and in Berlin 1926–1928 (as a student of Diels), where he submitted a dissertation *Analytische Studie über die Beziehungen der Phanerogamenflora* *von Arnhemsland (Nord-australien)*, published in *Beitr. Syst. Pfl.-Geogr. 5, Beih. Repert. Sp. Nov.* 51: 59–113 (1928). Later visiting professor in Turkey (1931–1934); director of the Haussknecht Herbarium and professor of botany at Jena (1946–1970). His main herbarium is at JE, with other material (probably not Australian collections) at ANK, B and KIEL.

References: Klotz, 1983; Hall, 1984; Stafleu & Cowan, 1985.

Portrait: Klotz, 1983.

Sieber, Franz W.

Born in Prague, (now Czech Republic), on 30 March 1789, and died there on 17 December 1844.

Travelled widely collecting plants in countries of Europe, the Middle East, southern Africa and Australia. Visited Port Jackson, New South Wales, for seven months from 1 June 1823 until December 1823 and assembled an exsiccatae of 645 local plants. A substantial number of Sieber's collections were acquired by MEL as part of the Steetz herbarium purchase. The most important collections of Sieber material are now in H, M, PR and W, but Stafleu & Cowan (1985) list 52 other herbaria containing some specimens.

References: Osborn, 1952; Hall, 1978; Ducker, 1981a, 1981b; Vallance, 1983; Short & Sinkora, 1988; Ducker, 1990; Short, 1990b; Olde & Marriott, 1994.

Portrait: Ducker, 1990.

Siemssen, G. Theodor

A merchant from Hamburg who visited Sydney (New South Wales) about 1838, and Port Adelaide (South Australia) in 1839, making some collections which were forwarded to Steetz. Siemssen was later a trustee for Steetz's widow and arranged for the sale of Steetz's herbarium (including his own collections) to MEL.

References: Kraehenbuehl, 1986; Short & Sinkora, 1988.

Simson, Augustus

Born in London, England, in 1836, died in Launceston, Tasmania, on 21 May 1918.

After a brief stay in Queensland, Simson moved to Tasmania in about 1873. A stock and share broker based in Launceston, Simson had interests in all branches of natural history. He collected extensively in Tasmania, mainly from mining areas, at least in the period May 1875–January 1893. He collected in north-eastern Tasmania (e.g. Goulds Country, Thomas Plain [Weldborough], Blue Tier) in the 1870s and 1880s and on the west coast in 1892–1893 (A.M.Buchanan, *pers. comm.*). His help was acknowledged by Rodway in *The Tasmanian Flora*. A large number of his collections were sent to Robert Sticht, a mining manager with the Mt Lyell Mining Co. from 1895 (Sticht died 30 April 1922, aged 65 years). The main part of this collection was deposited in HO about 1981. Other specimens are in JE, LE and NSW.

References: Scott, 1919; Buchanan, *pers. comm.*

Smith, Christopher

Visited Tasmania on *H.M.S. Providence* in 1792, collecting at Adventure Bay, Bruny Island, with James Wiles. The *Providence* and *Assistant* under the command of Captain William Bligh stayed at Adventure Bay from 9th until 24th February 1792. The main collection from this voyage is in BM, with duplicates in DPU, FI, G, HO and K.

Reference: Finney, 1984.

Smith, Sir James E.

Born in Norwich, England, on 2 December 1759, died in the same city, on 17 March 1828.

Trained in medicine and botany; lecturer in botany at Guy's Hospital, London, 1788–1796. Purchased Linnaeus' collections in 1784. Founded the Linnean Society in 1788 and was President until 1828. Published widely on Australian plants, of particular note being his contributions to John White's *Journal of a Voyage to New South Wales* (1790), his own *A Specimen of the Botany of New Holland...* (1793–1795) and 3348 articles in Rees' *Cyclopaedia* (1802–1820). Smith's herbarium contained collections by many others, including the following of particular importance to Australia: R.Brown, J.J.H. de Labillardière, C.Linnaeus, A.Menzies and J.White. The herbarium was bought by LINN in 1829, and is available on microfiche. A set of 268 Australian specimens is at LIV (colour transparencies held at CANB), particularly material of J.Banks, R.Brown, D.Burton, G.Caley, J.J.H. de Labillardière, A.Menzies, A.Phillip and J.White. Another set of duplicates is in MANCH (Conn, 1994), and some are at DBN (Nelson, 1996).

References: Maiden, 1908a; Hall, 1978; Edmondson, 1983; Stearn, 1988; Edmondson, 1993; Nelson, 1996.

Portraits: Hall, 1978; Mabberley, 1985.

Solander, Daniel S.

Born in Pitea, Sweden, on 19 February 1733, died in London, England, on 16 May 1782.

Pupil of Linnaeus; came to England in 1760. Assistant at the British Museum from 1763, Assistant librarian from 1765. Employed by Banks in 1768 to join him on Cook's first voyage to the Pacific. On their return in 1771 he became Banks' botanist/librarian and lived in his house at Soho Square. He described very little himself, but his specimens, manuscript notes and names have been used by others. His herbarium is now at BM, with some duplicates elsewhere, including AK, B, BRI, C, CAL, E, HAL, HO, MEL, MO, NSW, P, PERTH, P-JU, S, US, W, WELT.

References: Maiden, 1908a, 1921; Lyte, 1980; Finney, 1984; Olde & Marriott, 1994; Gascoigne, 1995; Duyker & Tingbrand, 1995; Duyker, 1998; Hansen & Wagner, 1998.

Portraits: Lyte, 1980; Duyker & Tingbrand, 1995; Gascoigne, 1995.

Sonder, Otto W.

Born (probably in Hamburg) in 1812, died in Hamburg, Germany, on 21 November 1881.

An apothecary in Hamburg, who accumulated an enormous private herbarium from some of the leading botanists and collectors of his day. He wrote the accounts of Epacridaceae, Stylidiaceae and algae in *Plantae Preissianae*, wrote an algal supplement to Mueller's *Fragmenta Phytographiae Australiae* and a major paper on Australian tropical algae, was co-editor with Harvey of *Flora Capensis*, wrote a local Flora, *Flora Hamburgensis*, and was editor and author of several families of *Plantae Muellerianae* in the journal *Linnaea*. He loaned his Australian herbarium to Bentham during compilation of *Flora Australiensis*. Sonder's herbarium was offered for sale during his lifetime, and after lengthy negotiations, the major part of it (perhaps 250 000 specimens) was purchased by MEL in 1883. The collection contained important algal specimens of Sonder, C.A.Agardh and W.H.Harvey, and flowering plant collections by C.F.Ecklon, J.G.C.Lehmann, C.P.Thunberg and C.L.P.Zeyher, as well as others associated with Martius's *Flora Brasiliensis*. Australian material of particular interest were a suite of Preiss collections, and duplicates received by Sonder from Ferdinand Mueller. Another major part of the Sonder herbarium, relating to African plants, is now at S (Stafleu & Cowan, 1985).

References: Maiden, 1921; M.Willis, 1949; Court, 1972; Nordenstam, 1980; Short, 1990b.

Portrait: Ducker, 1981a.

Spicer, W.W.

Born in Westminster, England, in 1820, died in Notting Hill, London, England, on 28 April 1879.

A clergyman, resident in Tasmania from about 1874 until April 1878. While there he was active in the Royal Society, wrote *Handbook of the Plants of Tasmania* (1878) the first locally produced Flora, and published a number of papers in the Royal Society journal. He collected many introduced plants, shunned by other early collectors, and these are often the earliest records of naturalisations in Tasmania. His Australian collections are in AK, DAO, E, HO, K, LIVU, MANCH and OXF.

References: Maiden, 1909a; Osborn, 1952.

Steetz, Joachim

Born 1804, died 1862.

A Hamburg-based botanist who accumulated a large herbarium from a variety of sources. This herbarium (of perhaps 5000 specimens) was purchased after his death by Ferdinand Mueller for the MEL herbarium. Australian collections in this herbarium were made by F.L.Bauer, J.W.T.L.Blandowski, J.Drummond, R.C.Gunn, J.J.H. de Labillardière, R.W.Lawrence, Leibolt , J.A.L.Preiss, F.W.Sieber and G.T.Siemssen. It also contained important non-Australian collections by, among others, J.D.Hooker and T.Thomson, B.Seeman and N.S.Turczaninov.

References: Short & Sinkora, 1988; Short, 1990b.

Story, George F.

Born in Carlisle, England, on 4 June 1800, died in Kelvedon, near Swansea, Tasmania, on 7 June 1887.

Appointed District Assistant Surgeon for Great Swanport, Tasmania, in April 1829, living at Kelvedon for most of his life. In charge of the Royal Society's Gardens in Hobart (1843–1847). Collected on the east coast of Tasmania for Mueller, and most of his collections are now to be found in MEL, with some in HO and M.

Reference: Maiden, 1909a.

Stuart, Charles

Born in England in 1802, died in Gosford, New South Wales, on 28 July 1877.

A gardener and collector, who is known to have been in Adelaide, South Australia, in 1847, where he met Ferdinand Mueller. He worked as a nurseryman/gardener and collected in Tasmania (1842 until about 1852), mainly at Perth, on the east coast and at Mt La Perouse. He sent most of his collections to Mueller at Adelaide, and these subsequently went with Mueller to MEL. He also collected algae for W.H.Harvey. Stuart left Tasmania about April 1852. He apparently returned for a time in about 1855–1857 (collections from Southport and La Perouse). Bentham (and Maiden, 1908a) noted that he later collected in the New England region of north-eastern New South Wales, where he was a gardener on a property near Tenterfield. Some of Stuart's Tasmanian collection became 'mixed' with those of Gunn and ended up in K. His New England collections went to Mueller (MEL) and some to Hooker (K). A few duplicates are in BM and HO, others in CN, E, FI, KIEL, LE, M, MANCH, O, TCD and W.

References: Maiden, 1908a, 1909a; Daley, 1935; Hall, 1978; Haegi, 1982; Buchanan, 1988b, 1990; Olde & Marriott, 1994; Conn, 1994.

Stuart, John McD.

Born in Dysart, Fife, Scotland, on 7 September 1815, died in London, England, on 5 June 1866.

Led five expeditions from Adelaide, South Australia, north across the country, between 1858 and 1862. Plants were collected on these journeys, and are now housed in BM and MEL.

References: Maiden, 1908c; Feeken *et al*., 1970; Hall, 1984; Kraehenbuehl, 1986; Cohn & Almond, 1991; Olde & Marriott, 1994.

Portraits: Feeken *et al*., 1970; Kraehenbuehl, 1986.

Map of expeditions: Cohn & Almond, 1991.

Symon, David E.

Born in London, England, on 13 October 1920.

A member of the staff of the Waite Institute, South Australia, from 1950 to 1985, holding numerous positions, including Reader in Agronomy. Under his direction the herbarium (ADW) expanded four-fold, largely as a result of his own extensive collecting in southern Australia. His research interests are wide-ranging, but with particular emphasis on Solanaceae, *Cassia*/*Senna*, *Oxalis*, plants of the Simpson Desert, *Trifolium subterraneum*, and more recently, Rosaceae. His herbarium of over 11 500 specimens was lodged at ADW, now transferred to AD, with duplicates elsewhere (e.g. B, NSW).

References: Hall, 1984; Gardner, 1990; Barker, 1997a.

Portrait: Gardner, 1990.

Tate, Ralph

Born in Alnick, Northumberland, England, in May 1840, died in Adelaide, South Australia, on 20 September 1901.

Appointed Elder Professor of Science at the University of Adelaide in 1875, teaching botany, zoology and geology. Collected from the last vestiges of the Adelaide Plains flora, and conducted a detailed survey in the South East (1882–1883). He wrote numerous papers on South Australian natural history, a *Census of the Flora of South Australia* (1880) and a *Handbook of the Flora of Extra Tropical South Australia* (1890). He published jointly with Mueller on the results of the Elder Exploring Expedition (see Helms) and participated in the Horn Expedition (1894). The botanical report of this expedition (1896) listed almost 500 plants, mainly from the vicinity of Uluṟu [Ayers Rock], Kata-Tjuta [Mt Olga], the George Gill Range, MacDonnell Ranges and the Finke River, Northern Territory. His herbarium at ADU was transferred on permanent loan to AD in 1954. A few duplicates are in K, MANCH and MEL.

References: Maiden, 1908c, 1912; Hall, 1978; Kraehenbuehl, 1983b, 1986; Conn, 1994.

Portrait: Kraehenbuehl, 1986.

Tepper, J.G. Otto

Born in Neutomischel, Posen, Prussia [Nowy Tomysl, Poland] on 19 April 1841, died in Norwood, South Australia, on 16 February 1923.

Came to South Australia in 1847. School teacher 1867–1883; Natural History Collector (1883–1888) and Entomologist (1888–1911) at the Adelaide Museum. Collected plants widely in the Murray Mallee, Barossa Valley, Mount Lofty Ranges, Yorke Peninsula and Kangaroo Island, and wrote a number of papers in a range of journals. His collections are now in AD (ex ADU) and MEL, with others in B, GOET, H, KIEL, M and MO. See also J.W.O.Tepper (his son), under Western Australia.

References: Kraehenbuehl, 1969; Hall, 1984; Kenneally, 1985; Kraehenbuehl, 1986.

Portraits: Kraehenbuehl, 1969, 1986.

Tepper, J.W.O.

Dates and places of birth and death unknown.

Telegraphist with the Post Office at Roebuck Bay, Western Australia, March 1889–1892, and son of J.G.O.Tepper (see under South Australia). He collected extensively at and near Roebuck Bay. He sent his collection of plants to his father, who forwarded them to Mueller for identification before publishing on them in 1893. His specimens are now at MEL, with some at PERTH, apparently received via the Western Australian Museum; others are at B and NSW (*Acacia*).

References: Kenneally, 1985; Kenneally *et al*., 1996.

Portrait: Kenneally *et al*., 1996.

Thozet, Anthelme

Born near Lyon, France, probably in 1826, died in Rockhampton, Queensland, on 31 May 1878.

Thozet was a gardener at the Sydney Botanic Gardens, New South Wales, in 1856–1858, before moving to Queensland. Collected extensively in the vicinity of Rockhampton, sending plants to F.Mueller. His main collections are now in MEL with lesser numbers in BR, G-DC, K, M, P and PC.

References: Maiden, 1910a, 1912; Froggatt, 1932; Hall, 1978.

Turczaninov, Nicholai S. (also transliterated as N.S.Turtchaninov)

Born in Nikiovka, Ukraine, in 1796, died 26 December 1863.

Turczaninov held a number of Government posts, particularly in Siberia. In later years at least some of his duties included scientific studies and botany, and he pursued these studies in retirement. He amassed a very large personal herbarium, including purchased material from Drummond (3rd collection), Preiss and Brown, and exchanged material with Hooker, Bentham and Steetz. Between 1846 and 1863 he published widely on Australian taxa (*inter alia*), based on the collections in his herbarium. He described 43 Australian genera and over 400 species, most from the collections of Drummond, but never visited Australia. His Australian specimens are now housed in KW, where 1059 Types of Australian taxa are stored in a separate collection.

Reference: Maiden, 1909b; Short & Sinkora, 1988; Marchant, 1990a.

Verreaux, Jules P.

Born in France on 24 August 1807, died, probably in England, on 7 September 1873.

An ornithologist and plant collector sent to Australia in 1842 by the Muséum d'Histoire Naturelle in Paris. He made plant collections around Hobart, Tasmania (December 1842–April 1844) and around Sydney, New South Wales (April 1844–November 1846). His servant Emile collected plants for him near Port Macquarie and Camden Haven, New South Wales, and also from the Moreton Bay district and Durundur, Queensland. He returned to France about 1851 with a reported 115 000 natural history specimens. His original herbarium is at P, with some at A, B, C, DBN, DS, E, G, GH, K, L, M, MO, OXF, PH, S and US.

References: Maiden, 1921; Michael, 1974; Roberts & Whitten, n.d.

Vickery, Joyce W.

Born in Sydney, New South Wales, in 1908, died there on 29 May 1979.

Vickery joined the staff of the National Herbarium of New South Wales in August 1936 as Assistant Botanist, rising to Senior Botanist by the time of her retirement. She was first editor of the herbarium's *Contributions* in 1939. Her research was almost entirely on the family Poaceae, with major contributions being a revision of *Poa* (1970) and the description of the whole family in *Flora of New South Wales* (1961, 1975). Issue 2(1) of *Telopea* (1980) was dedicated to her memory.

References: Johnson, 1980; Lee, 1980.

Portrait: Lee, 1980.

Vlamingh, Willem de

Born on the island of Vlieland, Netherlands, date unknown, date and place of death unknown.

Explored the Swan River (Western Australia) in 1697, and may be the collector of two specimens (*Acacia truncata* and *Synaphea spinulosa*) in G, erroneously described as ferns from 'Java'. If so, these are the earliest surviving herbarium specimens from Australia.

Reference: Feeken *et al.*, 1970; George, 1971, 1996b.

Portrait: Australia/Christmas Island 45c postage stamp of 1997.

Wakefield, Norman A.

Born in Romsey, Victoria, on 28 November 1918, died in Sherbrooke, Victoria, on 24 September 1972.

A school teacher with wide-ranging natural history interests, perhaps best known for his work on ferns, and the vegetation of East Gippsland, Victoria. Published *Ferns of Victoria and Tasmania* (1955, revised 1975). His collections are in MEL.

References: J.Willis, 1949b, 1949c, 1973; Aston, 1980; Hall, 1984; Cohn & Almond, 1991; Willis & Cohn, 1993.

Walter, Charles (Carl)

Born in Mecklenberg, Germany, c. 1831, died in Melbourne, Victoria, on 11 October 1907.

Arrived in Victoria in the 1850s. Probably accompanied Ellery's geodetic survey of East Gippsland and the New South Wales border 1869–1871. Later collected extensively in Victoria, particularly in the Alps, and in south-eastern New South Wales. Visited Samoa in 1875, Duke of York Island and New Britain (Bismarck Archipelago) with Rev. G.Brown in 1875. His collections were purchased by MEL in 1907. Duplicates are in B, E, G, KIEL, L, M, MICH, MO, NA, NMW, NSW, OXF and Z.

References: Anonymous, 1907; Maiden, 1908b; Hall, 1978; Short, 1990c; Willis & Cohn, 1993.

Warburton, Peter E.

Born in Northwich, Cheshire, England, on 16 August 1813, died in Beaumont, South Australia, on 5 November 1899.

Replaced Babbage on the Lake Torrens expedition of 1858. Some specimens, particularly from Mt Serle, South Australia, are in MEL. Other collections are from Venus Bay and the head of Spencer Gulf. Led another expedition from Alice Springs, Northern Territory, across the Great Sandy Desert to the Oakover River in Western Australia in 1872–1874.

References: Hall, 1984; Kraehenbuehl, 1986.

Portrait: Kraehenbuehl, 1986.

Waterhouse, John T.

Born, probably at Newcastle, New South Wales, on 2 December 1924, died in Gordon, New South Wales, on 1 April 1983.

On the staff of the Botany School, University of New South Wales from 1962, Senior Lecturer at the time of his death. Instrumental in developing the herbarium (UNSW), as well as carrying out floristic work in north-eastern New South Wales, and the Kakadu region of the Northern Territory. His taxonomic interests were in 'woody' monocotyledons, Asteraceae and Myrtaceae. His main herbarium is in UNSW.

References: Quinn, 1983, 1987; Hall, 1993.

Weber, Joseph Z.

Born in Cakovac (now Croatia) on 13 October 1930, died in Queensland on 14 March 1996.

Graduated from the University of Zagreb, and taught for eight years, before emigrating to Australia in 1965. He joined the staff of the State Herbarium of South Australia in 1966, retiring in 1995. His major research interests were in *Cassytha* and *Thelymitra*, and his collections are housed at AD, with duplicates distributed widely.

Reference: Jessop, 1996.

White, Cyril T.

Born in Kangaroo Point, Queensland, on 17 August 1890, died in Brisbane, Queensland, on 16 August 1950.

Grandson of F.M.Bailey, and nephew of J.F.Bailey, he succeeded the latter as Government Botanist in 1917, remaining in the position until his death. He had prepared the 976 line drawings in F.M.Bailey's *Comprehensive Catalogue of Queensland Plants* (2nd edn) (1913), and wrote extensively on the Queensland flora, in the fields of both taxonomy and economic botany. He was principally responsible for developing the Queensland Herbarium as a public institution, setting up networks of collectors, organising routine mounting of specimens, and insisting on adequate labelling. He established exchanges with other herbaria, particularly in the western Pacific. He collected widely in Queensland, and in all other Australian States (except the Northern Territory), New Caledonia (1923), New Guinea (1918, 1944, 1945) and the Solomon Islands (1945). His main herbarium is in BRI, but duplicates are widely distributed in, e.g. A, B, BM, C, DAO, E, F, GH, K, MEL, MO, NSW, NY, S and US.

References: Blake, 1952; Hall, 1978; Everist, 1982; Ingram, 1993; Olde & Marriott, 1994.

Portrait: Blake, 1952.

Bibliography: Blake, 1952.

White, John

Born about 1756, died in Worthing, Sussex, England, on 20 February 1832.

Appointed first Surgeon-General of New South Wales, arriving with the First Fleet in 1788, returning to England in 1794. He collected flora and fauna around Sydney, and in 1790 published *Journal of a Voyage to New South Wales* containing 65 engravings of plants, birds and animals. The plants forming the basis of this work were lodged in the herbarium of J.E.Smith, who collaborated in the work, and are now in LINN and LIV. Other White collections are reported from G, GH, NSW, PH and UPS.

References: Bailey, 1891; Maiden, 1908a; Hall, 1978; Finney, 1984; Edmondson, 1993.

White, Samuel A.

Born in Adelaide, South Australia, on 21 December 1870, died in Fulham, South Australia, on 20 January 1954.

An avid plant and bird collector. Collected along the Murray River in South Australia in 1877, in Queensland in 1891, and conducted a series of expeditions between 1911 and 1926 to north-eastern South Australia, Queensland and central Australia. The collections from several of these expeditions were described by J.M.Black, and are now in AD.

References: Hall, 1978; Kraehenbuehl, 1986.

Portrait: Kraehenbuehl, 1986.

Whittaker, Joseph

Born 1815, died 1894.

A nurseryman from Breadsall, Derbyshire, who collected 300 plants from the vicinity of Adelaide and from the southern Lofty Range to Encounter Bay, South Australia, in 1839–1840. This collection was purchased by W.J.Hooker and is now in K.

Reference: Kraehenbuehl, 1986.

Wilhelmi, J.F. Carl

Born in Dresden, Germany, in 1829, and died there in 1884.

A seedsman who arrived in Adelaide on 1 March 1849. He collected extensively in South Australia, particularly along the lower reaches of the Murray River to its mouth (1849–1851) and on Eyre Peninsula (1851) and the South East (1853). In 1854 he moved to Melbourne, Victoria, where he was Acting Government Botanist during Mueller's absence on the Gregory Expedition (1855–1856), and assistant to Mueller until 1869. In Victoria he collected in the Dandenongs, the mountains of western Victoria (the Grampians, Victoria Range, Pyrenees) and Corner Inlet in Gippsland. In November 1863 he briefly visited Sydney, New South Wales, making collections at Port Jackson. He returned to Germany in about 1865 or 1869 to resume business as a seedsman. His main collection of Australian plants is in MEL, with duplicates in B, BR, C, E, H, K, M, NA, OXF and W.

References: Maiden, 1908c, 1912; Hall, 1978; Kraehenbuehl, 1983b, 1990; Ross, 1995.

Portraits: Maiden, 1912; Kraehenbuehl, 1990; Willis & Cohn, 1993.

Wilkes, Charles – see A.Gray

Williamson, Herbert B.

Born in Beechworth, Victoria, on 18 June 1860, died in Melbourne, Victoria, on 30 January 1931.

A school teacher who took a life-long interest in natural history, and made many collections throughout Victoria. These are now housed in MEL and MELU, with duplicates elsewhere, including A, AK, E, F, G, K, KIEL, MO, NH and NSW. Honorary Keeper of the Herbarium at the Botany School, University of Melbourne from 1929–1931. Collaborated with Ewart in the production of *Flora of Victoria* (1931), and contributed the whole of Leguminosae. Published a monograph of *Pultenaea* (1920–1928) and a guide to Victorian ferns (1926).

References: J.Willis, 1949b; Hall, 1978; I.Clarke, 1990; Willis & Cohn, 1993; Olde & Marriott, 1994.

Portrait: Willis & Cohn, 1993.

Willis, James (Jim) H.

Born in Oakleigh, Victoria, on 28 January 1910, died in Melbourne, Victoria, on 10 November 1995.

Served as a forestry officer in many locations throughout Victoria, 1931–1937. In October 1937 Willis joined the National Herbarium of Victoria as a taxonomic botanist, and spent the remainder of his working life there, until 28 January 1972. He rose to become Assistant Government Botanist, and Acting Director of the Royal Botanic Gardens and Herbarium. Throughout his life he collected avidly, both vascular and non-vascular plants, and fungi. For many years he was the focus of taxonomic work in Victoria, and wrote the 2-volume *A Handbook to Plants in Victoria* (1962, 1972) which for over 30 years was the standard reference not only for that State but for adjacent areas as well. He described 64 plant species alone or jointly and published about 883 books, papers and reviews. His herbarium is housed in MEL, but duplicates are widely distributed within Australia and overseas.

References: Anonymous, 1975; Hall, 1978; Aston, 1995, 1996a; Aitken, 1997; Jack, 1998.

Portraits: Anonymous, 1975; Aston, 1996a; Aitken, 1997; Jack, 1998.

Map of collecting localities: Anonymous, 1975.

Woolls, William

Born in Winchester, England, on 30 March 1814, died in Burwood, New South Wales, on 14 March 1893.

Arrived in Sydney, New South Wales, in 1832, and became a master at The King's School, Parramatta; ordained as an Anglican Minister in 1873. Published a large number of papers in various newspapers and journals, and collected many specimens for Mueller. His two major works were *Plants Indigenous in the Neighbourhood of Sydney* (1880) and *The Plants of New South Wales* (1885). His original collections are housed at MEL and NSW, with some also in GOET and M.

References: Maiden, 1908a; Cable, 1976; Hall, 1978; Gilbert, 1985; Thompson, 1986.

Portraits: Gilbert, 1985; Thompson, 1986.

Brief biographical notes on the following botanists and collectors can be found as follows:

Francis Abbott [1834–1903] (Maiden, 1909)

Annie Adams (Mrs A.Wilson) [fl. 1889–] (Hammersley, 1981)

Frederick M. Adamson [fl. 1840s & 1850s] (J.Willis, 1949c; Hall, 1978; Willis & Cohn, 1993)

Robert S. Adamson [1885–1965] (Kraehenbuehl, 1986)

W. Allitt [1828–1893] (J.Willis, 1949c; Willis & Cohn, 1993)

H.W. Andrew [fl. c. 1900–1925] (Kraehenbuehl, 1983b, 1983c, 1986)

F.W. Andrews [fl. 1874–1875] (Kraehenbuehl, 1986)

Edwin Ashby [1861–1941] (Kraehenbuehl, 1986; Olde & Marriott, 1994)

James W.C. Audas [1872–1959] (J.Willis, 1949c, 1961; Kraehenbuehl, 1983b, 1983c; Willis & Cohn, 1993)

Robert Austin [fl. 1854–1856] (Maiden, 1921)

John Bailey [1800–1864] (Kraehenbuehl, 1986)

Bannier [fl. 1849–1851] (Kraehenbuehl, 1986)

Horace N. Barber [1914–1971] (Hall, 1978)

Thomas Barclay-Millar [fl. 1875–1923] (Bailey, 1891)

Francis G.A. Barnard [1857–1932] (Hall, 1978; Willis & Cohn, 1993)

John D. Batt [1843–1919] (Hall, 1978; Willis & Cohn, 1993; Short, 1997a)

George Bennett [1804–1893] (Maiden, 1908a)

Ken[d]rick H. Bennett [c. 1840–1891] (Maiden, 1908a)

Lewis A. Bernays [1831–1908] (Bailey, 1891; Maiden, 1910a)

Ernest Bethien [fl. 1888–1891] (Kraehenbuehl, 1986)

Wilfred A.W. de Beuzeville [1884–1954] (Hall, 1978)

Harriette S. Biddulph [1839–1940] (Bailey, 1891; Olde & Marriott, 1994)

Johann W.T.L. Blandowski [1822–?] (Kraehenbuehl, 1986)

William D. Brackenridge [1810–1893] (Maiden, 1908a)

Henry H.B. Bradley [1845–1918] (Maiden, 1921)

Arthur B. Braine [1854–1945] (J.Willis, 1949b; Willis & Cohn, 1993)

John H. Browne [1817–1904] (Kraehenbuehl, 1986, incl. portrait)

J. Stuart Browne [fl. 1875–1877] (Kraehenbuehl, 1986)

Robert Brummitt [1851–1927] (Kraehenbuehl, 1986)

Daniel Bunce [1813–1872] (Webster, 1980, incl. portrait; Kraehenbuehl, 1983b, 1983c, 1986; Fox, 1989, incl. portrait; Willis & Cohn, 1993)

J. Burkitt [fl. 1860s] (Kraehenbuehl, 1986)

R.C. Burton [fl. 1871–1890] (Bailey, 1891, Willis *et al*., 1986)

Julius H. Camfield [1852–1916] (Froggatt, 1932; Hall, 1978)

William A. Cannon [1870–1926] (Kraehenbuehl, 1986)

William Carron [1823–1876] (Maiden, 1908a)

William L. Cleland [1847–1918] (Kraehenbuehl, 1986)

G. Clowes [fl. 1850s] (Maiden, 1908a)

Robert Collie [1839–1892] (Maiden, 1908a)

Denis Considen [c. 1760–1815] (Maiden, 1908a; Hall, 1978)

Ernest F. Constable [1903–1986] (Hall, 1984; *Newslett. Austral. Syst. Bot. Soc*. 48: 24, 1986; Hall, 1993; Olde & Marriott, 1994)

Bruce J. Copley [1933–1984] (Hall, 1979; Olde & Marriott, 1994)

E. Cowley [fl. 1880s; Willis *et al*., 1986, cite an Ebeneezer Cowley, 1848/49–1889] (Bailey, 1891)

Alexander R. Crawford [1840–1912] (Maiden, 1921; Hall, 1978)

Robert L. Crocker [1914–1963] (Kraehenbuehl, 1983b, 1983c)

Mary A. Cronin (Mrs Mary Walters) [1871–1974] (Hammersley, 1981)

Michael Cronin [fl. 1884–] (Hammersley, 1981)

Edwin Daintrey [1814–1887] (Maiden, 1908a)

St Eloy D'Alton [1847–1930] (J.Willis, 1949c, with portrait; Willis & Cohn, 1993)

Richard H. Davies [fl. 1830s–1887] (Maiden, 1909)

Henry Deane [1847–1924] (Hall, 1978; Olde & Marriott, 1994)

Edmund A. Delisser [fl. 1861–1865] (Maiden, 1908c; Kraehenbuehl, 1986)

Andrew Dempster [1843–1909] (Hall, 1984)

Samuel Dixon [1841–1927] (Kraehenbuehl, 1983b, 1983c, 1986)

Francis S. Dutton [1816–1877] (Maiden, 1908c; Kraehenbuehl, 1986)

Misses Eaton (Hammersley, 1981)

Johann P. Eckert [1861–1924] (J.Willis, 1949c; Willis & Cohn, 1993)

August Engelhardt [fl. 1890s] (Kraehenbuehl, 1983b, 1983c, 1986)

Mrs W. England [fl. 1927] (Kraehenbuehl, 1983b, 1983c)

A.E. Errey [fl. pre-1914] (Kraehenbuehl, 1986)

Baron Constantin von Ettingshausen [1826–1897] (Hill, 1988; Olde & Marriott, 1994)

Thomas J. Ewing [1813–1882] (Maiden, 1909)

Hugh C. Fawcett [1812–1890] (Maiden, 1908a)

J. Felsted [fl. 1878–1879] (Kraehenbuehl, 1986)

John Fereday [1813–1871] (Maiden, 1909)

Barron Field [1786–1846] (Maiden, 1908a; Olde & Marriott, 1994)

James Fleming [fl. 1802–1804] (Maiden, 1908a)

Rev. J. Flierl (Kraehenbuehl, 1986)

Alexander G. Floyd [1926–] (Hall, 1984)

Alexander Forrest [fl. 1879] (Kenneally *et al*., 1996)

William Fowler [1820–1901] (Kraehenbuehl, 1986)

George W. Francis [1799–1865] (Maiden, 1908c; Kraehenbuehl, 1986, incl. portrait)

Charles French [1842–1933] (J.Willis, 1949b; Willis & Cohn, 1993)

James P. Fullagar [fl. 1860s–1870s] (Maiden, 1908a)

Walter Gill [1851–1929] (Hall, 1978; Kraehenbuehl, 1983b, 1983c, 1986)

[?] Gordon [fl. 1801] (Maiden, 1908a)

Jesse Gregson [1837–1919] (Hall, 1978)

Sir George Grey [1812–1898] (Maiden, 1909b; Kraehenbuehl, 1983b, 1983c, 1986)

Hubert H. D'A. Griffith [1877–1958] (Kraehenbuehl, 1986; Olde & Marriott, 1994)

H.A. Gunter [fl. 1932–1933] (Kraehenbuehl, 1986)

C.J. Gwyther [fl. 1880s] (Bailey, 1891)

Arthur A. Hamilton [1855–1929] (Froggatt, 1932; Olde & Marriott, 1994)

Edward D. Harrop [1828–1891] (Maiden, 1909)

Thomas S. Hart [1871–1960] (J.Willis, 1949c; Willis & Cohn, 1993)

Carl H. Hartmann [1833–1887] (Bailey, 1891; Robson, 1988)

Edwin Haviland [1823–1908] (Maiden, 1908a)

Desmond A. Herbert [1898–1976] (Hall, 1978, 1979)

Heinrich Heuzenroeder [1820–1898] (Maiden, 1908c; Kraehenbuehl, 1986)

Ernst B. Heyne [1825–1881] (Maiden, 1912; Willis & Cohn, 1993; Ross, 1995)

William Hillebrand [1821–1886] (Maiden, 1908c; Kraehenbuehl, 1986, incl. portrait)

Frank M. Hilton [fl. 1950s] (Kraehenbuehl, 1986)

Johann N. Hinteröcker [?–1872] (Kraehenbuehl, 1986)

Benedict P.G. Hochreutiner [1873–1959] (Kenneally *et al*., 1996)

Alfred Howitt [1830–1908] (Kraehenbuehl, 1986)

Doreen Hunt [fl. 1960s–1970s] (Kraehenbuehl, 1983b, 1983c)

William Hunter [1893–1971] (J.Willis, 1949c; Hall, 1984; Willis & Cohn, 1993)

Cyril K. Ingram [1912–] (Hall, 1978)

Eric N.S. Jackson [fl. 1950s–1997] (Barker, 1997b)

Nora Jacob [fl. 1907] (Kraehenbuehl, 1983b, 1983c)

George Jacobson [fl. 1880s–1890s] (Bailey, 1891)

Alexander W. Jessep [1892–1991] (Churchill, 1991; Ross, 1991a)

Charles F. Johncock [fl. 1902] (Kraehenbuehl, 1986)

C.W. Johns [fl. 1938] (Kraehenbuehl, 1986)

Robert D. Johnston [1922–] (Hall, 1978)

Oliver L. Jones [1849–1933] (Hall, 1984)

W.R. Kefford [fl. 1880s] (Bailey, 1891)

James Keys [fl. 1880s] (Bailey, 1891)

James Kidd [1800–1867] (Maiden, 1908a; Froggatt, 1932)

Philip P. King [1793–1856] (Maiden, 1908a; Olde & Marriott, 1994)

Richard Kippist [1812–1882] (Maiden, 1909b; Olde & Marriott, 1994)

Friedrich E.H.W. Krichauff [1824–1904] (Maiden, 1908c; Kraehenbuehl, 1986)

Charles E. Lane-Poole [1885–1970] (Kenneally *et al*., 1996, with portrait)

Charles J. La Trobe [1801–1875] (Willis & Cohn, 1993; Olde & Marriott, 1994)

Joseph Lauterer [1848–1911] (Bailey, 1891; Maiden, 1921)

John W. Lewin [?1770–1819] (Maiden, 1908a, 1921)

Lind [fl. 1873–1874] (Maiden, 1908a)

David Lindsay [1856–1922] (Kraehenbuehl, 1986)

Johann G.W. Luehmann [1843–1904] (Hall, 1978; Willis & Cohn, 1993)

Lieutenant R. Lynd [1800–1851] (Maiden, 1908a)

William Macarthur [1800–1882] (Maiden, 1908a; Hall, 1978; Olde & Marriott, 1994)

John Maclean [fl. 1829–1836] (Maiden, 1908a; Froggatt, 1932)

Alexander Macleay [1767–1848] (Maiden, 1908a)

William S. Macleay [1792–1865] (Maiden, 1908a; Olde & Marriott, 1994)

W. Alexander Macpherson [fl. 1877–1897] (Bailey, 1891; Maiden, 1910a)

W.T. Malpas [fl. 1850] (Kraehenbuehl, 1986)

James Martin [fl. 1863–1864] (Olde & Marriott, 1994; Kenneally *et al*., 1996)

Hugh S. McKee [1912–1995] (Olde & Marriott, 1994; *Newslett. Austral. Syst. Bot. Soc.* 82: 12, 1995)

J.N. McKibbin [fl. 1880s] (J.Willis, 1949b; Willis & Cohn, 1993)

James O. McWilliam [1808–1862] (Maiden, 1908a)

O.E. Menzel [fl. 1890–1910] (Hall, 1984; Kraehenbuehl, 1986)

Louisa A. Meredith [1812–1895] (Maiden, 1909; Martin, 1996)

Fanny E. De Mole [1835–1866] (Maiden, 1912)

William Morrison [fl. 1824–1828] (Maiden, 1909b)

William L. Morton [1820–1898] (Hall, 1978; Willis & Cohn, 1993; Albrecht, 1996, with portrait)

Samuel Mossman [fl. 1850s] (Edmondson, 1983)

Robert Mudie [1777–1882] (Hall, 1978; Mabberley, 1992)

Theodor R. Müller [fl. 1862–1869] (Willis & Cohn, 1993; Ross, 1995)

B. Jean Murray [fl. 1927–1931] (Kraehenbuehl, 1986)

James P. Murray [fl. 1861–1862] (Kraehenbuehl, 1986)

Simpson Newland [1835–1925] (Kraehenbuehl, 1986)

Francis W. Newman [?1796–1859] (Maiden, 1909)

A. Norton [fl. 1880s] (Bailey, 1891)

James Norton [1824–1906] (Maiden, 1908a)

Theodore G.B. Osborn [1887–1973] (Kraehenbuehl, 1986)

Ferdinand Osswald [fl. early 1850s] (Kraehenbuehl, 1986)

Edward Palmer [1833–?1899] (Bailey, 1891)

David J. Paton [1891–1941] (Hall, 1984; J.Willis, 1949c; Willis & Cohn, 1993)

Reuben T. Patton [1883–1962] (Willis & Cohn, 1993)

Roy Pearce [1921–1995] (*Newslett. Austral. Syst. Bot. Soc*. 84: 28, 1995)

W. Anthony Persieh [1826–?1880s] (Bailey, 1891)

Edward E. Pescott [1872–1954] (J.Willis, 1949b; J.Willis, 1949c; Willis & Cohn, 1993)

William Phillips [1803–1871] (Maiden, 1921)

C.F. Plant [fl. 1880s] (Bailey, 1891)

Alexander Purdie [1859–1905] (Maiden, 1909b; Olde & Marriott, 1994)

B.S. Roach [fl. early 1900s](Kraehenbuehl, 1986)

John G. Robertson [1803–1862] (J.Willis, 1949c; Kraehenbuehl, 1983b, 1986; Buchanan, 1988b; Willis & Cohn, 1993; Roberts & Whitten, n.d.)

William N. Robertson [?–1844] (Maiden, 1908a, Froggatt, 1932)

George A. Robinson [1788–1866] (Willis & Cohn, 1993)

Augustus Rudder [1828–1904] (Maiden, 1908a; Hall, 1978)

Miss Salmon [fl. 1869] (Kraehenbuehl, 1986)

W.A. Sayer [fl. 1886–1897] (Hall, 1978)

Sebastian Schauer [fl. 1841–1847] (Thompson, 1989)

Henry Schneider [fl. 1891–1917] (Bailey, 1891)

Ludwig W. Schulzen [fl. 1848–1857] (Kraehenbuehl, 1983b, 1983c, 1986)

Benedict Scortechini [1845–1886] (Bailey, 1891; Maiden, 1910a; Olde & Marriott, 1994)

Thomas Scott [1800–1855] (Maiden, 1909)

Edmund G. Sealey [1823–1864] (Maiden, 1908c; Kraehenbuehl, 1986)

Martha Sewell (Hammersley, 1981)

William S. Sharland [fl. 1832] (Maiden, 1909)

Patrick L.C. Shepherd [1831–1903] (Maiden, 1908a; Olde & Marriott, 1994)

Thomas Shepherd [1780–1835] (Maiden, 1908a; Olde & Marriott, 1994)

Thomas W. Shepherd [1824–1884] (Maiden, 1908a)

Mrs Shipway [fl. 1905] (Kraehenbuehl, 1983b, 1983c)

Lindsay S. Smith [1918–1970] (Ingram, 1993; Olde & Marriott, 1994)

Anthony *(Tony)* ***G. Spooner*** [1927–1997] (Bell, 1998)

Thomas Stackhouse [?–1886] (Maiden, 1908a)

Karl T. Staiger [1833–1888] (Hall, 1978; ?Robson, 1988, as 'Steiger')

William Stephenson [fl. 1845–c. 1863] (Maiden, 1908a)

James Stirling [1791–1865] (Maiden, 1909b)

James Stirling [1852–1905] (J.Willis, 1949c; Willis & Cohn, 1993)

Frederick Strange [1826?–1854] (Maiden, 1908a)

Charles Stuart [1802–1877] (Kraehenbuehl, 1986; Olde & Marriott, 1994)

J.W.R. Stuart [fl. 1884] (Bailey, 1891)

D. Sullivan [?–1895] (J.Willis, 1949c; Willis & Cohn, 1993)

Richard F. Sullivan [fl. late 1800s] (Kraehenbuehl, 1986)

Charles S. Sutton [1863–1950] (J.Willis, 1949c; Willis & Cohn, 1993)

William Swainson [1789–1855] (Maiden, 1912; Maroske & Cohn, 1991; Willis & Cohn, 1993)

Robert Sweet [1783–1835] (Maiden, 1908a; Olde & Marriott, 1994)

Alfred J. Tadgell [1863–1949] (J.Willis, 1949c; Willis & Cohn, 1993; Olde & Marriott, 1994)

William H. Tietkens [1844–1933] (Maiden, 1908c; Hall, 1984; Kraehenbuehl, 1986)

Henry T.N. Tisdall [1836–1905] (Willis & Cohn, 1993)

Henry Tryon [1856–1943] (Bailey, 1891)

George E. Turner [1810–1869] (Maiden, 1908a)

William Vernon [1811–1890] (Maiden, 1908a)

Nathaniel Vicary [fl. 1835–1853] (Maiden, 1908a)

Pemberton Walcott [c. 1835–1883] (Maiden, 1909b; Hall, 1984; Olde & Marriott, 1994)

James Walker [1794–1854] (Maiden, 1908a)

Frederick G. Waterhouse [1815–1898] (Maiden, 1908c; Kraehenbuehl, 1986; Olde & Marriott, 1994)

William Waterman [fl. 1846–1852] (Maiden, 1908a)

George Watkins [?–1916] (Bailey, 1891)

Thomas Watling [1762–1806] (Maiden, 1908a)

Clara Wehl [1833–1901] (Kraehenbuehl, 1983b, 1983c, 1986)

Louisa Wehl [fl. early 1880s] (Kraehenbuehl, 1986)

Wheeler [fl. 1861–1862] (Kraehenbuehl, 1986)

James F. Wilcox [1823–1881] (Maiden, 1908a)

Thomas B. Wilson [1792–1843] (Hammersley, 1981; Olde & Marriott, 1994)

Charles G.A. Winnecke [1856–1902] (Maiden, 1908c; Kraehenbuehl, 1986)

Joseph G. Wood [1900–1959] (Kraehenbuehl, 1986)

Julian E. Tenison Woods [1832–1889] (Maiden, 1908c; Kraehenbuehl, 1983b, 1983c, 1986)

Collin E. Woolcock [1914–1990] (Ross, 1990, incl. portrait; Olde & Marriott, 1994)

Walter J. Zimmer [1898–1967] (J.Willis, 1949c; Willis & Cohn, 1993).

Brief biographical notes on contemporary botanists can be found as follows:

Laurence G. Adams [1929–] (Hall, 1984, 1989)

David E. Albrecht [1962–] (Hall, 1992; Olde & Marriott, 1994)

George N. Batianoff [1945–] (Hall, 1984)

Anthony R. Bean [1957–] (Hall, 1989, 1992)

David J. Bedford [1952–] (*Newslett. Austral. Syst. Bot. Soc*. 72: 20–21, 1992)

Eleanor M. Bennett [1942–] (Hall, 1978)

Douglas H. Benson [1949–] (Hall, 1992)

Donald F. Blaxell [1934–] (Hall, 1978, 1992; Olde & Marriott, 1994)

Douglas J. Boland [1947–] (Hall, 1984, 1989)

Desmond E. Boyland [1941–] (Hall, 1984)

Barbara G. Briggs [1934–] (Hall, 1992; Olde & Marriott, 1994)

John D. Briggs [1954–] (Hall, 1989; Olde & Marriott, 1994)

John Brock [1951–] (Hall, 1993)

M. Ian H. Brooker [1934–] (Hall, 1978)

Jeremy Bruhl [1956–] (*Newslett. Austral. Syst. Bot. Soc*. 73: 7, 1992)

Alexander K. Cameron [1908–] (Hall, 1978)

Denis J. Carr [1915–] (Hall, 1978; Hall, 1989; see also under Maisie Carr)

Carrick T. Chambers [1930–] (Polglase, 1996)

John R. Clarkson [1950–] (Hall, 1989; *Newslett. Austral. Syst. Bot. Soc.* 78: 10–11, 1994)

Barry Conn [1948–] (*Newslett. Austral. Syst. Bot. Soc.* 67: 30–33, 1991; Olde & Marriott, 1994)

Alec B. Costin [1925–] (Hall, 1984)

Arthur Court [1927–] (Canning, 1989; Hall, 1984)

Robert G. Coveny [1943–] (Hall, 1984; Olde & Marriott, 1994)

Lyndley A. Craven [1945–] (Hall, 1993; Olde & Marriott, 1994)

Michael D. Crisp [1950–] (*Newslett. Austral. Syst. Bot. Soc*. 71: 22–25, 1992)

Andrew Douglas [fl. 1994–1997] (*Newslett. Austral. Syst. Bot. Soc*. 80: 25, 1994)

Clyde R. Dunlop [1946–] (Hall, 1984; Olde & Marriott, 1994)

Don Foreman [1945–] (*Newslett. Austral. Syst. Bot. Soc.* 66: 21, 1991)

Paul I. Forster [1961–] (Hall, 1992, 1993)

Alan M. Gray [1943–] (Hall, 1979)

Gordon P. Guymer [1953–] (Hall, 1984, 1993)

Rodney J.F. Henderson [1938–] (*Newslett. Austral. Syst. Bot. Soc.* 64: 17 (1990), incl. portrait)

Kenneth D. Hill [1948–] (Hall, 1992)

Stephen D. Hopper [1951–] (Hall, 1989)

Bernard P.M. Hyland [1937–] (Hall, 1989)

Betsy R. Jackes [1935–] (Hall, 1984)

Robert W. Johnson [1930–] (Hall, 1984; Simon, 1990, incl. portrait)

Gregory J. Keighery [1950–] (Olde & Marriott, 1994)

Kevin F. Kenneally [1945–] (Hall, 1984; Olde & Marriott, 1994)

Phillip G. Kodela [1962–] (Hall, 1993)

Pauline Y. Ladiges [1948–] (Hall, 1992)

Nicholas S. Lander [1948–] (Hall, 1984)

Peter J. Lang [1955–] (Hall, 1992)

Peter K. Latz [1941–] (Hall, 1984; *Newslett. Austral. Syst. Bot. Soc.* 81: 24 (1994), incl. portrait)

Michael Lazarides [1928–] (Hall, 1984; Olde & Marriott, 1994)

Greg Leach [1952–] (*Newslett. Austral. Syst. Bot. Soc.* 66: 22, 1991; Hall, 1993)

Terry D. Macfarlane [1953–] (*Newslett. Austral. Syst. Bot. Soc.* 64: 21, 1990)

Robert O. Makinson [1956–] (Hall, 1992; Olde & Marriott, 1994)

Bruce R. Maslin [1946–] (Hall, 1978; Olde & Marriott, 1994)

T. John McDonald [1935–] (Hall, 1984)

Donald G. McGillivray [1935–] (Olde & Marriott, 1994, with portrait)

David Morrison [1958–] (*Newslett. Austral. Syst. Bot. Soc.* 66: 22, 1991)

Desmond J. Nelson [1935–] (Hall, 1984)

Wolfgang *(Wally)* ***F. Pataczek*** [1932–] (Hall, 1984)

Leslie Pedley [1930–] (Hall, 1984)

John Pickard [1944–] (Hall, 1984)

Jocelyn Powell [1939–] (*Newslett. Austral. Syst. Bot. Soc.* 66: 21, 1991)

Christopher F. Puttock [1954–] (Hall, 1993; *Newslett. Austral. Syst. Bot. Soc.* 78: 9–10, 1994)

Philip R. Sharpe [1915–] (Hall, 1984)

Raymond V. Smith [1923–] (Hall, 1984; Olde & Marriott, 1994)

Raymond L. Specht [1924–] (Hall, 1984)

Joan M. Taylor [1929–] (Hall, 1989)

Mary D. Tindale [1920–] (Hall, 1984; Olde & Marriott, 1994)

Malcolm E. Trudgen [1951–] (Hall, 1984)

Leonard J. Webb [1920–] (Hall, 1984)

David J.E. Whibley [1926–] (Hall, 1984)

Trevor P. Whiffin [1947–] (Hall, 1989; Hall, 1992)

Barbara Wiecek [1958–] (*Newslett. Austral. Syst. Bot. Soc*. 66: 22, 1991)

Glenn M. Wightman [1961–] (Hall, 1992)

John B. Williams [1932–] (Hall, 1992; Olde & Marriott, 1994)

Paul G. Wilson [1928–] (Hall, 1989; Olde & Marriott, 1994).

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Acknowledgments

The compiler is most grateful to the many people who read and commented on the first draft of this chapter. In particular, thanks are due to Laurie Adams, Alex Buchanan, Lyn Craven, Winifred Curtis, Clyde Dunlop, Murray Fagg, Alex George, Gordon Guymer, Rod Henderson, Helen Hewson, Pauline Ladiges, Neville Marchant, Dennis Morris, John Parham, Chris Puttock, Andrew Rozefelds, Annette Wilson and Karen Wilson.

DEVELOPMENT OF THE *FLORA OF AUSTRALIA* PROJECT

A.S.George[1], A.McCusker[2] & A.E.Orchard[3]

Historical background

The project to write a *Flora of Australia* is the first of its kind in this country. Only one previous Australia-wide Flora has been undertaken, *Flora Australiensis* (1863–1878), written during the colonial period by George Bentham who never visited Australia. The new *Flora* is the most exciting botanical project undertaken in Australia. It had a long gestation and a difficult birth; its completion, like that of works such as de Candolle's great *Prodromus* (1823–1878) and Martius' *Flora Brasiliensis* (1840–1906), will be a major achievement of national and international co-operation.

Bentham's *Flora* and plans for its revision

Like all Floras, Bentham's *Flora Australiensis* was out of date by the time the last volume was published. The seven volumes spanned 16 years, and were written entirely by George Bentham. Bentham based his Flora on the collections at Kew, the British Museum, the Linnean Society, and the Jardin des Plantes, Paris, as well as specimens sent on loan from Melbourne by Ferdinand Mueller, Government Botanist of the Colony of Victoria, and other loans from Hamburg (Sonder) and Vienna (Bauer, Fenzl, Hügel). During this period botanical work was expanding in Australia. Field collectors were active, many encouraged by Mueller, himself a prodigious collector and then at the peak of a long and productive career.

Bentham had planned to publish a supplement to *Flora Australiensis* but, in the preface to Volume 7, he wrote that it '*would entail more labour than at my age it would be prudent to undertake*'; he was then 78. Instead, he encouraged Mueller to produce a complete census of the flora. Mueller accomplished this by 1882 and revised it in 1889.

Colonial Floras (State Floras after Federation in 1901), mostly extracted from *Flora Australiensis* with the addition of species discovered later, were issued over the succeeding years in all States except Western Australia, where a systematic census prepared by the Government Botanist Charles Gardner was issued in 1930–1931. Most of these Floras were compiled by professional taxonomists employed by State Governments or by universities. These botanists were few in number and other demands on their time were such that they were often able to do little research to underpin their Flora-writing. By the early years of the 20th century, however, the first of many accomplished amateur taxonomists to contribute to the literature on the Australian flora had appeared on the scene. J.M.Black, a retired journalist, published *The Naturalised Flora of South Australia* in 1909, followed by his *Flora of South Australia* in 1922–1929. The latter is currently in its fourth edition, now under the editorship of John Jessop, Chief Botanist of the State Herbarium of South Australia.

Long after Federation the States continued to work completely independently in the fields of botanical exploration and description of their floras.

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National collaboration begins through ANZAAS

Throughout most of the 20th century the periodic Congresses of the Australian and New Zealand Association for the Advancement of Science (ANZAAS), and its forerunner the Australasian Association for the Advancement of Science, have been important meeting places for professional scientists from the research institutes, universities and government agencies on both sides of the Tasman Sea. For many years ANZAAS was the only regular forum for discussion among Australian plant taxonomists.

The first reference to a new national Flora for Australia appears to be that in 1907 by Joseph Maiden, Government Botanist and Director of the Botanic Gardens, Sydney. In his Presidential Address to Section D (Biology) at the eleventh meeting of the Australasian Association for the Advancement of Science, he suggested that each State should issue supplements to *Flora Australiensis,* and went on to say:

> '*The form of the new 'Flora Australiensis' (which cannot be published until western Australia is more thoroughly explored botanically) will then fitly take the form of the most modern classification available, which, at the present moment, is of course that of Engler, although even that fine arrangement need not be slavishly followed in every detail.*
>
> *We in Australia suffer much through our geographical isolation from the great intellectual centres of the Northern Hemisphere. That is our misfortune, but we should not fail in our endeavours to advance knowledge of the botany of this continent, and potent help in this direction would be the issue of an 'Australian Flora' based on the most modern lines of taxonomic research, modified, indeed, by our own special knowledge of our own plants and their affinities.*'

Nine years later, however, Maiden acknowledged that a new Flora was some time off. In the preface to the *Census of New South Wales Plants* (1916), which he compiled jointly with Ernst Betche, he wrote that Bentham's *Flora Australiensis*

> '*is, and will long remain, the standard work on our flora. The greater one's experience with it, the more sincere is one's admiration of it*'.

Generations of Australian taxonomists have echoed Maiden's admiration of this work but its value as a standard reference was eroded over the years as more and more species were discovered. While the need for a new Flora was discussed occasionally, there seems to have been no attempt to fulfil that need during the first half of the 20th century. Throughout this period most of the botanists with major interests in collecting and describing plant species were employed by the State Governments. Even after the Second World War the staff of State herbaria were still preoccupied with collecting, preparation of State Floras, and individual lines of research confined within their respective State borders. Without the interest and co-operation of the States a new national Flora would have been impossible.

At the 25th meeting of ANZAAS (Adelaide, August 1946) a meeting of plant taxonomists recommended the formation of a Systematic Botany Committee. The meeting listed, under 'immediately desirable tasks', the 'preparation of floras, especially for some States'. There was no resolution regarding a national Flora. The new Committee fostered communication within the taxonomic community by issuing a newsletter entitled *Australasian Herbarium News.* In the first issue, of June 1947, a Commonwealth Government scientist, William Hartley, Senior Plant Introduction Officer with CSIRO, called for the establishment of a new Commonwealth Herbarium which could facilitate the preparation of a national Flora (Hartley, 1947). He envisaged that the Flora would be prepared by many botanists from the various States, with the Commonwealth Government funding replacement staff during their period of commitment.

William Hartley's appeal, though almost prophetic of longer-term developments, failed to arouse much interest at that time. The next meeting of ANZAAS, in Perth, August 1947, again urged progress with State floras. This attitude, as stated by Stanley Blake, a senior botanist with the Queensland Herbarium, persisted up to the 31st Meeting at Melbourne in 1955, at which '*an attempt to do something more definite [about a national Flora] ... met* *with little response*' (Blake, 1960). The *Australasian Herbarium News*, during the eight years that it was published, carried no further reference to a Flora of Australia.

The initial impetus to the campaign which finally led to the current *Flora of Australia* project came from a newcomer to the Australian botanical scene, Hansjoerg Eichler. In 1957, less than two years after arriving from Germany to take up the position of Keeper in the State Herbarium of South Australia, Eichler recommended that his staff be permitted to undertake Australia-wide revisions which could be used towards a new *Flora of Australia*. This required a major change in policy. Joseph G. Wood, then Professor of Botany at the University of Adelaide and Chairman of the Handbooks Committee of the Flora and Fauna of South Australia, immediately took up the suggestion for a national Flora and had it placed on the agenda for the 33rd ANZAAS Congress, held in Adelaide in August 1958. This time the topic aroused extensive discussion, during which it became clear that opinion was divided on the level of detail that would be appropriate for a Flora. There was support on the one hand for a monographic approach, based on full revision of all groups, and on the other for a concise treatment based solely on existing published knowledge. Eichler proposed the creation of a central taxonomic unit with 10 botanists producing revisional studies for a Flora.

Significantly, however, ANZAAS resolved to set up a Flora of Australia Committee 'to prepare estimates and detailed plans of the organisation required for the preparation of a new Flora Australiensis'. The Flora of Australia Committee consisted of R.T.M.Pescott (Convener), S.T.Blake, D.J.Carr, Hj.Eichler, L.A.S.Johnson, S.Smith-White and D.E.Symon. At its first meeting, Melbourne, 22–25 April 1959, Blake was elected Chairman. Following intensive debate, a report was prepared recommending that a monographic work be produced, to be called *Flora of Australia*. The Blake Committee had considered but dismissed the concept of a Flora based only on existing published knowledge, as not serving 'any useful purpose' (Blake, 1960). The idea of a generic Flora was also rejected on the grounds that it would hinder the preparation of a full Flora, and because it was considered that genera could not be properly delimited until the species were better known. The Committee's report envisaged that the Flora would be produced over a period of about twenty years by a central organisation with a staff of fourteen taxonomists under the direction of an Editor-in-Chief. It suggested that the organisation might be at Canberra, possibly with some of the taxonomists stationed at existing herbaria or universities, similar to the model put forward by Hartley twelve years earlier!

The Academy of Science supports the cause

The Flora of Australia Committee's report was adopted by ANZAAS at the 34th Congress in Perth, August 1959. A delegation from ANZAAS in July 1960 presented it to the Prime Minister's Department, which in turn referred it to the Australian Academy of Science, a body of Australia's most distinguished scientists, established in 1954 and highly regarded by the Federal Government as a source of advice on issues of science policy.

The Academy, recognising the need not only for a Flora but also for a similar study of the Australian fauna, recommended to the Prime Minister of the day, the Right Honourable Sir Robert Menzies, that a Museum of Australian Biology be established with the principal aims of conducting a biological survey of Australia and writing a 'comprehensive multi-volume Flora of Australia'. The Government at that time was unable to finance the museum, although it did not dispute the need for such a development.

The 1960s saw great economic development in Australia, especially in agriculture, mining and manufacturing. At the same time awareness of the environmental effects of these industries became more widespread, leading to a great surge of public concern for the natural environment. In the public and private sectors, the need for environmental surveys in both settled and remote areas placed great demands on the services of botanists and made the lack of a national Flora even more apparent. During the same period horticultural interest in the indigenous flora also increased markedly.

Development of the Flora of Australia project

A facsimile edition of Bentham's *Flora Australiensis,* published by Asher and Reeve in 1967, drew international attention to the lack of a modern *Flora* (Stafleu, 1967). In April that year the Prime Minister referred to the Academy of Science a further plea from ANZAAS expressing regret at the lack of support for a new Flora and emphasising the importance of the project. The Academy appointed a Flora and Fauna Committee to examine it.

In 1970 and 1971 events occurred that greatly stimulated discussion of a new Flora and led to the commencement of preliminary work for it. To celebrate the bicentenary of James Cook's first landing in Australia in 1770, William Stearn, a distinguished botanist with the British Museum (Natural History), was invited to address the Academy. Stearn used his address to highlight the conspicuous absence of a modern Australian Flora and to underline the urgent need to write one. He was later approached confidentially by Sir Maurice Mawby, Director of Conzinc Riotinto of Australia Limited and a Fellow of the Academy, who offered to raise private funds to help launch work on a new Flora. Stearn referred Sir Maurice to John Beard, then Director of the Royal Botanic Gardens, Sydney.

Beard, who in previous discussions had favoured a concise Flora along the lines of *Flora Europaea,* now drew up a new proposal for regional Floras to cover Australia in the four phytogeographic regions (South-eastern, Tropical, Eremean and South-western) as proposed by Burbidge, (1960). Beard envisaged that these Floras would be written in five years, possibly by staff in the various State and Commonwealth herbaria.

Sir Maurice's offer to assist was conditional upon support for the project being received from both the Academy and the Australian botanical community. It soon became clear that Australian plant taxonomists were by no means united in support of Beard's proposal. It was not seen as a means of reducing the duplication and taxonomic confusion that existed across State borders (the boundaries between phytogeographic regions being less precise than political boundaries), or as a reference work to assist in the later production of a more complete national Flora and more critical State Floras. Most taxonomists believed that even such apparently simple texts would require the critical research that was lacking for many genera (Burbidge, 1974). Various alternative proposals were made, e.g. for a generic Flora, a series of monographs and an index of Australian plant names, but there was widespread dissension as to how to proceed.

It was with some frustration that Sir Maurice wrote in these terms to Stearn in July 1971 to report on the progress of his initiative:

> '*... there appears to be complete disagreement as to how such a task should be tackled. ... quite frankly, I am completely at a loss to understand why there cannot be a unanimous desire to produce such a worthwhile reference.*'

However, the Stearn/Mawby initiative had already begun to bear fruit. After further discussions at the 43rd ANZAAS Congress in Brisbane, May 1971, three proposals which could be commenced with the funds likely to be made available as a result of Sir Maurice's initiative, were submitted to the Academy of Science for consideration: an Australian Plant Name Index, a Generic Flora of Australia, and a series of Handbooks for regions not then covered by other floristic works. It was envisaged that the first would provide basic data for a new Flora, the second would be a valuable source of information on the flora and an expansion of the *Dictionary of Australian Plant Genera* (Burbidge, 1963), while the third would fill the gaps in the field of Australian regional floras.

In response to these proposals the Academy, in November 1971, set up a Standing Committee for a Flora of Australia under the chairmanship of David G. Catcheside, Director, Research School of Biological Sciences, Australian National University. His committee consisted of an experienced, active taxonomist from each State and the Australian Capital Territory and six botanists from Australian universities.

Meanwhile, a group of Adelaide taxonomists, led by Eichler, circulated a comprehensive questionnaire to all Australian plant taxonomists, over half of whom responded. Of these, about 80% preferred the initial production of an Australian Plant Name Index. With the assurance of such a high level of support from botanists for the Australian Plant Name Index

(APNI) proposal, the Catcheside Committee decided to initiate this project using the funds made available to the Academy through Sir Maurice Mawby.

Nancy Burbidge was released from her duties as Curator of the CSIRO herbarium to lead and plan the Academy's 'Flora Project'. Compilation of APNI commenced in April 1973 with the appointment as bibliographer of Penelope Hack, who was succeeded in January 1974 by Arthur Chapman. Nancy Burbidge brought up to date her earlier list of taxonomic literature available in Australian libraries (Burbidge, 1951, 1978). She also commissioned three sample treatments for a Flora text, to be made available for discussion. The largest of these, Brassicaceae by Helen Hewson, was initiated in 1974–1975 using part of the Mawby funds. The Academy administered the project financially until 1976 and CSIRO supported it by making available research and library facilities. Eichler took up the Curatorship of the CSIRO herbarium. Thus CSIRO was able to report, among its 1973 achievements:

> '*We have at last a project which enables some advance towards the long term goal of a new Flora of Australia*.'

Throughout the period leading to the final decision to proceed with a new Flora, made seven years later, the Academy continued to give strong support to the concept. During that period the need for a new Flora became ever more urgent and, importantly, more obvious not just to the scientific community but to a much wider section of the Australian public.

Requirements for a viable Flora project

To embark on the production of a new Flora of Australia three components would be necessary: a concept, an institutional arrangement, and secure financial support. The community of plant taxonomists, through ANZAAS, had grappled with the concept but no agreement had yet emerged. The Academy of Science had begun to come to terms with the institutional requirement and, having among its fellows a sprinkling of leading scientists from the business sector, was also conscious of financial realities and would eventually become the major player in securing financial support. Important groundwork for a Flora of Australia was at last under way. The major national scientific bodies, the Australian Academy of Science and CSIRO had worked together to reach this stage, but long-term financial and institutional support for the preparation of a new Flora of Australia was not yet in sight.

A biological survey of Australia

As early as 1969 Sir Macfarlane Burnet, as President of the Academy, had led a delegation to the Minister for Education and Science to press the claim for establishment of a Biological Survey of Australia. In May 1972 the Academy of Science wrote to the Minister for Education and Science requesting reconsideration of the proposal. Further support came in the same year from a House of Representatives Select Committee on Wildlife Conservation (Fox, 1972, Waterhouse, 1978).

The Academy's Flora and Fauna Committee, having a broader brief, had extended the discussion beyond the scope of a new Flora. In 1968 it canvassed the various State museums and found general support for a Commonwealth biological survey. The Flora and Fauna Committee released a report in October 1968 in which it proposed that an organisation, to be called a Biological Survey of Australia, be established (Anon., 1968; Summary & Recommendations published as Fenner, 1969). The Survey was to initiate the production of a new Flora of Australia. It was suggested that existing herbaria in Canberra might form the basis of the botanical collections to be used for writing a national Flora. At that time there were separate small herbaria in CSIRO, the Forest Research Institute, the Botanic Gardens and the Australian National University. The Committee considered that collaboration with herbaria in the States would be essential.

The growth of an active conservation movement in Australia in the early 1970s widened the demand for information on biological resources. Increasing public enthusiasm for the horticultural use of native plants, and the burgeoning of an active amateur group, the Society for Growing Australian Plants (SGAP) (established 1958) whose members were acutely aware of the need for accurate names and data on the native plants used in horticulture, increased the pressure on the Commonwealth Government to begin producing a national Flora. These parallel developments were highly significant in that they created widespread demand from an informed public sector for scientific information on the Australian flora and fauna which, at that time, was not readily available. The need for a biological survey had now become sufficiently important for the major Australian political parties to include it in their platforms for the Federal Election in 1972 (Ride, 1978).

Interim Council of the Australian Biological Resources Study

In 1973 the Government took the first step towards implementing a national biological survey when it established the Interim Council of the Australian Biological Resources Study (ABRS). The Council's functions were:

(a) Initially, to promote through grants to existing State and Commonwealth institutions:

- the collection and scientific description (taxonomy) of species of animals and plants throughout Australia;
- in-depth studies of the ecology of such species; and
- proper maintenance of collections.

(b) After a few years of operations, to consider and make recommendations in relation to:

- conduct in the longer term of taxonomic and ecological studies; and
- housing, maintenance and display of national scientific collections (Waterhouse, 1978).

The Interim Council was allocated $750 000 for a three-year program. On the botanical side, grants were made for taxonomic and ecological studies and for the curation of collections. This initial grants program was the forerunner of the ABRS Participatory Program, which is now a major source of funding specifically targetting taxonomy.

The clear preference among State taxonomists was for the Flora preparation to be based in Canberra at the Herbarium Australiense in the CSIRO Division of Plant Industry. The Division of Plant Industry, however, including its taxonomic staff (except Dr Burbidge who was nearing retirement), did not favour this arrangement. Some Herbarium Australiense staff favoured the option of a new CSIRO division wholly for taxonomic research, but the senior management of the Division of Plant Industry was not convinced that this alternative would afford taxonomic research on plants as much security and resources as it was then receiving. The Division of Plant Industry advised ABRS of its position in July 1975. The ABRS Interim Council, which would also have preferred the Herbarium Australiense as the base for a long-term Flora project, was thus forced to consider other options.

In establishing ABRS within the Department of Science, the Government determined, *de facto*, an institutional affiliation for the Flora of Australia which was not among the possibilities canvassed in any of the previous discussions. A unit to support the Interim Council, and headed by the inaugural Director of ABRS, David Ride, was established not within CSIRO but within the Commonwealth Department of Science, although Dr Ride himself was a CSIRO scientist on secondment to the Department. The Bureau of Flora and Fauna, which eventually launched the *Flora of Australia*, had its origins in this unit.

Applications for grants from the $0.75 million made available by the Government exceeded $7 million! It was not possible, of course, even to consider directing grant funds towards facilitating the writing of a new Australian Flora other than in the most general way because the direction of the project had yet to be defined. Nearly all the grants for plant taxonomy were made in support of monographic studies, without specifying that the output should be directed specifically towards producing a Flora treatment.

In March 1975 the ABRS Interim Council received a report from the Academy of Science on the projects commenced with the Mawby funds, seeking financial assistance to continue them beyond June 1975. The Council resolved to provide financial assistance to the Academy to allow it to complete the projects. In its report to the Government, the Council considered making provision for the Flora of Australia project to be incorporated in the long-term institutional arrangement that it would recommend for the Australian Biological Resources Study. Following Dr Burbidge's death in 1977 the Academy project was continued by two of her staff, Arthur Chapman and Helen Hewson, both of whom were later to become key staff of the Bureau of Flora and Fauna. (Chapman completed the APNI, which was published by ABRS in 4 volumes in 1991. Hewson was engaged initially as an in-house Flora writer and went on to become Director of Flora in ABRS). At the 1975 meeting of the Interim Council the wider question, whether ABRS would take over the role of the preparation of the Flora, as initially envisaged by the Academy, was placed firmly on the table.

ABRS becalmed

The Interim Council of ABRS presented its report to the Government late in 1975. It contained recommendations for continuation of the biological resources study. It also recommended that the Government allocate substantial resources to a properly planned program of taxonomic and directly associated work and emphasised the essential role of Commonwealth Government support. The recommended objectives included a Flora of Australia, along with an Australian Faunal Directory and an Australian Biotaxonomic Information System.

Regrettably, the report was launched on the eve of one of the most tumultuous political events in Australian history – the dismissal by the Governor General of the Whitlam Government. Despite the commitment of the incoming (Fraser) Government, in its electoral platform, to a national biological survey, it was understandably very difficult to attract the new Government's attention to this topic in the short term. The report was referred by the Government to an Administrative Review Committee and a Committee on Co-ordination of Support for the Collection of Data on the Flora and Fauna of Australia. The question of the location of ABRS within the Commonwealth Public Service was considered by the Science Task Force of the Royal Commission on Australian Government Administration. The Interim Council's scientific recommendations were referred to the Academy of Science and to the Government's chief scientific advisory body, the Australian Science and Technology Council (ASTEC) to be reviewed and re-reviewed. In its report for 1976–1977, ASTEC recommended the establishment of a new body, the Institute of Australian Flora and Fauna (IAFF), to 'support and co-ordinate publication of a systematic series of regional floral handbooks'. It recommended that existing ABRS staff be incorporated into the new Institute. ASTEC saw the initial role of the IAFF, in relation to flora, as one of ensuring consistency in regional Floras, preparing and co-ordinating index volumes, and supporting taxonomic studies and handbooks. This, it was said, would pave the way for writing a more complete Flora when appropriate funds became available.

Meanwhile, ABRS was placed in a 'holding pattern' with minimal levels of annual funding, but without long-term commitment. A further entreaty to the Government to continue funding ABRS and to commence a Flora came in December 1977 from the Committee of Heads of Australian Herbaria.

ABRS prepares for the *Flora*

From 1975 onwards ABRS began to act as a focal point for continuing attempts to plan and cost a Flora. Despite the flurry of activity over the years since Stearn's visit, and the numerous plans and preparatory works, no proposal for writing a Flora of Australia had yet been submitted to the Government. A note of frustration appeared in the report of the Systematic Botany Committee of ANZAAS in 1976:

> '*The time lost on the Flora project since concrete proposals for it were submitted in 1959 is of scientific concern: progress in all fields of botany dealing with Australian plants ... is severely hampered by the inadequacy of taxonomic knowledge ... and the lack of a comprehensive work in which modern knowledge is made readily available*'.

Development of the Flora of Australia project

A visit to Australia in 1973 by C.G.G.J. van Steenis, then Director of the Rijksherbarium, Leiden, had focused attention on the scope and organisation of flora writing through discussion of *Flora Malesiana* (1948–). There was still a deep divergence of opinion about the nature of the Flora to be produced, the sample treatments prepared in the Academy project proving ineffective in resolving the matter. Indeed, few people had shifted from their original (in some cases 1950s) views. Van Steenis strongly preferred a concise flora, but some of the senior local voices still wanted a monographic work.

Neither was ABRS much nearer to obtaining a good estimate of the size of the flora, and therefore to agreeing on the resources likely to be required for whatever model was chosen. The ANZAAS Flora of Australia Committee had suggested that the Australian (vascular) flora contained over 15 000 species and that a monographic treatment would amount to 30 000 pages (Blake, 1960). A somewhat clearer picture of the state of taxonomic knowledge of the Australian flora was gradually built up. In an assessment in the early 1970s, Burbidge estimated that 25 families of flowering plants were sufficiently well known to be written up for a Flora; 73 small families could also be written up without detailed research; 84 families required revision in most genera; seven could be written up at a non-critical level; and 33 were of doubtful position (Burbidge, 1974). In 1978 a survey conducted by ABRS revealed that only 37 of the 222 flowering plant families recognised by Burbidge were being actively studied in Australian herbaria (Ride & McCusker, 1978). Although there was doubt as to the final format of the Flora, it was felt that a work based on current knowledge would quickly lose value and that a 'vigorous modern Bentham' was needed urgently to get on with the job (Ride, 1978).

Based on the fairly imprecise goals of '*producing a Flora acceptable to professional taxonomists in a reasonable time at a cost that one could envisage being acceptable to a future government*', and taking into account the then current rate of taxonomic research output in Australia, the task was estimated to require 25 dedicated taxonomists to achieve an output of 1000 species per year. This estimate (Paul Wilson, Senior Botanist with the Western Australian Herbarium, unpublished, written about May 1975) was based on a flora of 25 000 species. Further groundwork for a Flora was undertaken by Wilson while on secondment to ABRS in 1976. He prepared a set of *Guidelines for Contributors to a Flora* which were widely circulated for comment among Australian taxonomists. Although prepared for a Flora published in family parts, the Guidelines nonetheless contributed significantly to the format eventually adopted.

The years 1976 and 1977 were a very lean period for the ABRS grants program and the Director and staff were in no position to raise public expectations of a long-term commitment by the Government. However, this provided an ideal opportunity for the botanical staff to begin to draft a blue-print for a definitive Flora of Australia program that could be put forward for approval, should the Government suddenly decide to commit the minimum viable level of resources that had been recommended by ASTEC. These resources needed to be sufficient to meet the ever-increasing demand for collated information to support environmental assessments and management studies, and to convert the dreams and expectations of two or three generations of Australian plant taxonomists into reality.

There was an unwritten assumption that the Flora of Australia would commence with the vascular plants and, in particular, with the flowering plants. Accordingly, ABRS botanists of the time, Alison McCusker and John Busby, began to compile a list of the species of the flowering plants of Australia as a working document to estimate, as reliably as possible, the size of the task and the likely number of volumes. Compiling a national species list was a very difficult challenge at that time. Only one State, Queensland, had most of its herbarium collection computerised and all State and Territory herbaria held large amounts of undetermined material of many genera. The laborious task of extracting names from the indexes of the most recent regional floras was continued until a consolidated list of over 13 000 names, believed to represent currently recognised species, was obtained. It was roughly estimated, on the basis of a more detailed survey of a few large genera, that this list comprised about two-thirds of the total flora. Thus, the estimates of resources required to write a flowering plant Flora were based on a rough but realistic estimate of 20 000–22 000 species.

During the 1970s, however, real progress had been made in breaking down the isolation that had existed since before Federation between taxonomic botanists employed by the various State Governments. Communication and co-operation between Australian botanists received a boost with the formation in April 1973 of the Australian Systematic Botany Society (ASBS). First proposed by a group of Victorian botanists, the Society rapidly gained a membership of over 200 and in 1997 had over 300 members. The Society immediately began to collate information on an Australia-wide basis, first preparing an index to current plant taxonomic research in Australia (Whiffin, 1979).

In 1973 a Committee (later Council) of Heads of Australian Herbaria (CHAH) was formed, by decision of the Commonwealth/State Standing Committee on Agriculture, '*to promote all matters of interest to herbaria in Australia and to increase cooperation and understanding between them*'. CHAH has continued to index plant taxonomic research (Johnson, 1975; Johnson, 1976; Johnson & Goodchild, 1981; Johnson & Halford, 1987; Cowley & Puttock, 1993; Puttock & Cowley, 1997).

In 1976 John Jessop, who had succeeded Eichler as head of the State Herbarium of South Australia, proposed that ASBS co-ordinate and edit a *Flora of Central Australia*. Despite some initial concern that this project might lessen support for a national Flora, it went ahead and was substantially completed before work on the *Flora of Australia* commenced. The *Flora of Central Australia* (Jessop, 1981), prepared by over 50 contributors in three years, covers a major geographical region of the continent but, with about 2000 species, includes only 10% of the Australian flora. This project proved to be a useful forerunner of a national Flora, insofar as it broke the ground of interstate collaboration in plant taxonomy and gave many people experience in flora-writing.

Permanent establishment of ABRS

The question of a biological survey of Australia, including the preparation of a national *Flora*, had been under scrutiny for two decades when, in August 1977, Senator the Honourable James Webster, then Minister for Science, announced that ABRS would continue as an established program and that one of its three areas of research would be work in preparation for a *Flora of Australia*. The encouragement generated by this announcement was short-lived; further action by the Government was very slow to follow. It was not until 4 December 1978 that the Minister for Science announced the appointment of the new ABRS Advisory Committee, saying that '*the establishment of the Committee was a great step forward in continuing the success of the biological survey program*'. By the end of the 1978–1979 financial year, more than a year after the decision was announced to establish ABRS permanently, nothing had been done to implement it beyond appointing a distinguished Advisory Committee and maintaining the operation at a level of funding which, in real terms, was less than half that provided in 1975–1976 for the third year of the Interim program ($433 800 in 1975–1976; $250 000 in 1978–1979). It was not until December 1979 that the Bureau of Flora and Fauna was formally established as a branch of the Department of Science and the Environment.

Flora of Australia project established

At its first meeting, 6–8 March 1979, the ABRS Advisory Committee, after reviewing the progress made on co-ordinating index volumes and regional flora handbooks, resolved to advise the Minister (then the Minister for Science and the Environment) that it was now appropriate for a modest start on the *Flora* to be made and that, consequent on the Minister's approval, it would proceed forthwith. The Advisory Committee also resolved to appoint an Editorial Committee of five senior botanists (one member of the Advisory Committee and four others) and to have a Prospectus on the *Flora of Australia*, with sample texts, published for distribution at the XIII International Botanical Congress in Sydney in August 1981. The Advisory Committee also agreed to continue work on the Australian Plant Name Index and the Australian Plant List (the Census). The proposed Plant Taxonomic Revision Series was given 'low to medium priority', and never proceeded.

Given the financial position of ABRS in March 1979 these were ambitious plans. But the very existence of such plans placed additional pressure on the Government to give adequate support to the program. The Committee's recommendation was accepted by Senator Webster, and the commencement of the *Flora of Australia* project was announced on 24 April 1979. Further support was to come soon afterwards in the form of a letter to the Prime Minister, the Right Honourable Malcolm Fraser, from the Council of the Australian Conservation Foundation, calling on him to use his personal influence to increase the funding of ABRS. Although ABRS had been established as a program to increase scientific knowledge of the flora and fauna, Fraser was well aware of its value to conservation and environmental studies. Indeed, he himself, as Minister for Science some years earlier, had spoken strongly in its favour to a meeting of Commonwealth-State Conservation Ministers because of its value to conservation. His personal support is believed to have been important, later, in securing the Government approval and level of resources that would make the launching of the *Flora of Australia* at the XIII International Botanical Congress a reality.

The Advisory Committee, perhaps mindful of the events that followed Beard's 'regional handbooks' proposal, agreed that consultation with botanists was essential and resolved that, consequent on the Minister's approval of the commencement of the Flora, the botanical public be informed that the Committee was beginning to write a concise *Flora of Australia* and was seeking advice on the scope, format and content. In the previous two decades of debate support in the botanical community had moved, to some extent, towards a revisionary Flora that seemed likely to be beyond the long-term financial commitment that any government could be reasonably expected to make, but nothing had been resolved. It was clear that choices would have to be made with the utmost diplomacy. ABRS staff drew up a list of points on which decisions would have to be made and circulated it to all herbaria, university departments of botany, and practising higher plant taxonomists, canvassing their views. The intention was to follow the majority view on points where there was a clear majority and to propose the most logical compromise where there was not.

The response was good, numerically, but it proved impossible to formulate a realistic proposal based on majority preferences on dozens of individual points. The dilemma is illustrated by the fact that a large majority opted for publication in case-bound volumes, but also preferred to have each family issued separately. With the species list showing that there were about 75 families of flowering plants represented in Australia by 5 species or fewer, it was clearly impractical to adopt the majority view on both these points! The prospective publishers, initially the Australian Government Publishing Service, strongly preferred substantial volumes as being more practical for marketing, so the choice was made on that basis. It led, however, to the need for a system in which to arrange the families. This proved to be the most contentious issue of all.

In October 1979 a Flora Study Group was appointed under the Chairmanship of Sir Rutherford Robertson, Chairman of the ABRS Advisory Committee and Vice-Chairman of ASTEC. The Study Group wasted no time in determining the scope, arrangement and format of the *Flora*. Several systems of classification were considered, the use of a phylogenetic system being preferred to any other arrangement because it would provide a definite framework and prevent groups from being neglected. The system of Arthur J. Cronquist (Cronquist, 1981), then at a late stage of revision, was chosen for the *Flora*. Based on this system, a scheme for the number and content of the volumes was devised. The Committee felt that the time needed to prepare a monographic Flora was unacceptable, but planned the work so that groups in urgent need of revision could be studied before the relevant volumes were issued. Meanwhile, the scope and format were discussed at length among the taxonomic community.

In April 1980 the ABRS Advisory Committee endorsed a set of general recommendations concerning production of the *Flora* which fixed the format of the *Flora*: bound volumes with the families arranged according to Cronquist's classification, the volumes numbered consecutively but produced in the most convenient sequence. The Flora Study Group was reconstituted as an Editorial Committee to advise on writing the *Flora*. The composition of the Editorial Committee over the years is listed elsewhere in this volume. It was stipulated that writers would review the current state of taxonomic knowledge, examine specimens and cite representative specimens, but would not undertake detailed revisionary work. It was recommended that writing proceed at a rate that would allow the publication of 3 volumes per year (a goal which has not been realised due to resource constraints), and that the Advisory Committee itself take account of the *Flora* writing schedule when determining the Preferred Objectives for ABRS grants. This last point, although not popular with taxonomists at the time, has been instrumental in causing many of Australia's taxonomists to schedule their research output to feed into the *Flora of Australia* program and, unquestionably, has improved both the quality and rate of production of the *Flora*.

Wishing the Bureau of Flora and Fauna to benefit, as much as possible, from the experience of institutions with recent experience in writing other major national or continental floras, the Advisory Committee approved a recommendation to the Department for a Government-sponsored visit to institutions in the United States and Europe to discuss the *Flora of Australia* in the light of their experiences. This visit, which was undertaken by the then ABRS Director of Flora, Alison McCusker, in June–July 1980, yielded valuable information and insight into aspects of project management, costing, production and market identification.

Alex George, formerly of the Western Australian Herbarium, was appointed Executive Editor of the *Flora of Australia* in January 1981 and the Bureau of Flora and Fauna succeeded in meeting its first target, the publication of Volume 1 in time for the launching of the *Flora of Australia* at the XIIIth International Botanical Congress in Sydney in August 1981.

Progress of the Flora of Australia project

By many standards, the project to write a new *Flora of Australia* has been successful. Since its launch in 1981 twenty volumes have been published (see Table 5), and nearly 40 000 copies have been sold. Some 140 contributors have described and provided keys to over 6000 species. Contributions to 25 further volumes have been received by ABRS and several of these are well-advanced. Substantial funding has been provided through the ABRS Participatory Program to support taxonomic work, and this has had important spinoffs to State and regional Floras as well as advancing the national project.

Like many government programs, ABRS has moved from one home to another as governments and administrative arrangements have changed. When a Department of Science and the Environment was created in 1979, ABRS joined it as part of the Science component, but was soon transferred to the Environment division. Science and Environment subsequently parted company and ABRS has developed and evolved within the government's Environment arm, losing one of its original components with the formation of the Environmental Resources Information Network (ERIN) as a separate entity in 1989. Both ABRS and ERIN were transferred in 1990 to the Australian National Parks and Wildlife Service (ANPWS) under the direction of Dr Peter Bridgewater, a former Director of the Bureau of Flora and Fauna. ANPWS (later, Australian Nature Conservation Agency (ANCA)), in turn, was absorbed into the more expansive Environment Australia (Department of the Environment and Heritage) in 1996, as part of the Biodiversity Group.

In tandem with these administrative changes, the *Flora of Australia* headquarters migrated around Canberra for a decade before settling, appropriately, at the Australian National Botanic Gardens in 1989. The previously separate herbaria of the Canberra Botanic Gardens and CSIRO (CBG and CANB) amalgamated in 1994 as the core of the Centre for Plant Biodiversity Research (CPBR), and is the main reference collection used by Flora program staff.

In a major review of ABRS in 1991/1992, Professor David Green, Chief Science Adviser to the Minister for the Environment, strongly commended the ABRS program as having '*increased urgency and relevance in the context of the National Strategy for Conservation of Biodiversity and Ecologically Sustainable Development*' (Green, 1992).

Despite the many changes in administrative arrangements, it has been possible to achieve continuity for the *Flora of Australia* program. Successive Ministers have relied on the advice of the Flora Editorial Committee and the ABRS Advisory Committee in determining priorities for publication of the *Flora* and funding of research to underpin the writing. The foundation Executive Editor, Alex George, remained with the program until January 1993 when he was succeeded by Dr Tony Orchard who, as Curator of the Tasmanian Herbarium, had already been a major collaborator. The Flora Editorial Committee, since its formation in 1980, has had five chairmen: Sir Rutherford Robertson (1980–1981), Dr Barbara Briggs (1982–1987), Dr Jim Ross (1988–1993), Dr Judy West (1994–1995) and Dr Michael Crisp (1996–) all of whom had already had long and close associations with the *Flora* program. These factors have enabled Australia to produce a national *Flora* of uniform standard and style, a major challenge for a series issued over nearly two (and eventually at least three) decades.

Communication among taxonomists in Australia, and between Australia and overseas, has improved steadily, partly generated by the national *Flora* project, and certainly strengthening collaboration with it. When the *Flora* project commenced in 1979, ABRS assumed administrative responsibility for the position of Australian Botanical Liaison Officer (ABLO) at the Royal Botanic Gardens, Kew, UK. The ABLO arrangement, initiated in 1937, provides for Australian taxonomic botanists to be based at Kew on one-year appointments. As the main destination to which early Australian plant collections were sent for safekeeping, and the institution in which Bentham's *Flora Australiensis* was written, Kew has a critical contribution to make to the new *Flora of Australia* and the ABLO provides a crucial link between Australian taxonomists and this key institution.

An annual ABRS newsletter, *Biologue*, was launched in 1983, and has been expanded progressively to provide information on ABRS activities. In 1998 it was distributed to about 1000 individuals and institutions world-wide. In 1997 ABRS established a homepage on the World Wide Web to provide another avenue of information on its activities.

Table 5. *Flora of Australia*: volumes published (to November 1998).

Volume	Title	Publication date
1	Introduction	22 August 1981
3	Hamamelidales to Casuarinales	24 April 1989
4	Phytolaccaceae to Chenopodiaceae	12 November 1984
8	Lecythidales to Batales	9 December 1982
12	Mimosaceae (excl. *Acacia*), Caesalpiniaceae	4 May 1998
16	Elaeagnaceae, Proteaceae 1	30 November 1995
18	Podostemaceae to Combretaceae	8 June 1990
19	Myrtaceae — *Eucalyptus*, *Angophora*	27 June 1988
22	Rhizophorales to Celastrales	17 May 1984
25	Melianthaceae to Simaroubaceae	25 December 1985
28	Gentianales	28 June 1996
29	Solanaceae	27 July 1982
35	Brunoniaceae, Goodeniaceae	6 August 1992
45	Hydatellaceae to Liliaceae	15 May 1987
46	Iridaceae to Dioscoreaceae	2 May 1986
48	Ferns, Gymnosperms and Allied Groups	27 October 1998
49	Oceanic Islands 1	3 May 1994
50	Oceanic Islands 2	29 July 1993
54	Lichens — Introduction, Lecanorales 1	4 September 1992
55	Lichens — Lecanorales 2, Parmeliaceae	21 December 1994

ABRS also became the focal point for the publication of other Australia-wide taxonomic works. In 1984 it launched a series of occasional publications, the *Australian Flora and Fauna Series*. Over the next seven years 15 volumes were published in this series, 14 of them on flora. They include the *Census of Australian Vascular Plants*, the *Australian Plant Name Index*, and a number of important baseline bibliographic works on mosses, liverworts and lichens. The *Australian Flora and Fauna Series* was discontinued in 1991, but a need still existed for a vehicle for publication of basic bibliographic, monographic and biogeographic works, preliminary to compilation of *Flora of Australia* and other handbooks. In 1994 the *Flora of Australia Supplementary Series* was launched, and seven titles have been published to April 1997, with others in preparation.

In September 1994 the Flora Editorial Committee decided that the fungi and algae, originally planned to be included in *Flora of Australia*, should be described in two separate series, to be called *Fungi of Australia* and *Algae of Australia*. This decision was based on recent developments in taxonomic theory. Since 1981 it has become increasingly apparent that the old view of a two-Kingdom natural world (plants and animals) can no longer be sustained, and several new classification schemes which recognise several Kingdoms have been proposed. Although new concepts of relationships are by no means fully resolved it has become clear that Algae and Fungi are far removed from vascular plants. The Editorial Committee's decision was endorsed by the ABRS Advisory Committee, and the first two parts (together forming Volume 1) of *Fungi of Australia* were published in 1996. The third book in the series was published in 1997.

The *Flora of Australia* project has made a significant practical contribution to the knowledge of Australia's plant biodiversity. The series is widely distributed and extensively used in libraries throughout Australia and abroad. The *Flora of Australia* is recognised internationally as one of the best of its kind (Schmid, 1997), and the Australian Biological Resources Study is hailed as a far-sighted and efficient program (Hoagland, 1996). Perhaps one of the greatest accolades for the *Flora of Australia* has been that of Veldkamp (1988):

> '*The series should be studied well by those that contemplate writing floras, for it is exemplary of how it should be done.*'

Current state of knowledge of the Australian flora

The Australian flora is still far from being adequately known. *Flora Australiensis* contained 8125 species of vascular plants. In 1981 the number of vascular plants was unknown but estimated to be about 18 000 species (George, 1981); in addition there were thought to be several thousand non-vascular species. In 1990 the *Census of Australian Vascular Plants* (Hnatiuk, 1990) revealed 17 590 named vascular species, and a further indeterminate number recognised by State herbaria but not yet formally named. Significant increases will result as taxonomic revisions and more thorough botanical exploration continue. A sample of genera and sections of genera that have been revised in Australia during the past 40 years shows that the average increase in species when such revisions are made is just under 50 per cent. The sample may not be representative in that workers may have selected genera known to contain large numbers of undescribed species, although it included revisions of genera in which few new species came to light, e.g. *Phebalium* (4 new species in a total of 45) and *Terminalia* (2 in 29). On the other hand, in a revision of *Synaphea*, George (1995) recognised 50 species, of which 37 were new and a further 2 were newly-raised to species level.

Of the non-vascular taxa which will be included in *Flora of Australia*, estimates in 1997 put the numbers of mosses at about 1100 species, liverworts at about 500 species and the lichens at about 2500 species. These numbers undoubtedly will increase also as research continues.

Few parts of Australia have been fully explored botanically. New species and records continue to be turned up, even near closely settled areas, and there are very large areas (thousands of square kilometres) where no work at all has been done. This applies especially to parts of the north and to Western Australia. Collecting in such regions will in general extend the range of known species, but new discoveries are certain to be made. Alien taxa continue to become naturalised. In an analysis of the Victorian flora, for example, Ross (1976) calculated that the rate of introduction and establishment of non-Australian species to that State had averaged five to six species per year over the previous 100 years. Jessop & Toelken (1986) recorded an average increase of 26 species per year to the known flora of South Australia in the period 1957–1984, including both native and naturalised taxa. There is little doubt that the Australian vascular flora eventually will be found to contain over 25 000 species.

Since the early 1990s an important threat to progress in cataloguing and understanding Australia's biodiversity has become apparent: the decline in numbers of, and support and training for, Australian taxonomists. This problem was first addressed by a Symposium held at the Australian Academy of Science, sponsored by the Australian Institute of Biology, on 11–12 November 1991. The proceedings of the Symposium were published as a special issue of *Australian Biologist* (Tyndale-Biscoe, 1992). Findings of the Symposium were measured against a baseline survey of taxonomic resources in Australia in 1975 (Ride & McCusker, 1978). Among the more worrying aspects identified were an inadequate level of curation of the nation's museum and herbarium collections and a declining funding base to address this (Armstrong, 1992), a significant decline in the numbers of taxonomists employed (Richardson & McKenzie, 1992), and weaknesses in training programs (Ladiges, 1992).

Such problems are not confined to Australia. Barry Conn (1994) reported on concerns with loss of biodiversity in the Pacific region, the inadequacy of inventories and the lack of taxonomic resources to address the problem. On a wider scale, *Systematics Agenda 2000* (Anonymous, 1994) made the same points for the world as a whole.

In 1995 ABRS sponsored a workshop in Canberra to review the status of taxonomy since the Academy Symposium of 1991. This workshop (Visher, 1996) found that, far from improving, the situation had become worse. The number of systematists on university teaching staffs had continued to decline, teaching of tertiary courses in systematics was also declining, fewer students were proceeding to postgraduate studies in taxonomy, practising taxonomists were becoming fewer, and their average age was increasing, job opportunities were shrinking, and large gaps in available expertise (particularly in non-vascular plants and invertebrate animals) were not being filled.

Steps are being taken to remedy the situation. On 18 June 1993, Australia ratified the international *Convention on Biological Diversity*, and shortly afterwards released a *National Strategy for the Conservation of Australia's Biological Diversity*. This document recognises, *inter alia*, the need to accelerate research into the taxonomy, geographic distribution and evolutionary relationships of Australia's biota, and states that this can best be achieved by strengthening the role of the Australian Biological Resources Study. ABRS has addressed the decline in taxonomic resources in Australia in a number of ways, particularly through the Participatory Program grants scheme. Many grants under the Participatory Program scheme have supported postgraduate students and technical officers while they gained experience in taxonomic research, and since 1994 Postgraduate Scholarships in taxonomy have been offered. However, additional and more widely-sourced resources will be needed in future if Australia is to compile a comprehensive inventory of its natural heritage in a timely manner.

In 1998 ABRS was co-sponsor of a meeting in Darwin, which produced *The Darwin Declaration* (Anonymous, 1998). This document draws attention to the global crisis in taxonomic resources (the 'Taxonomic Impediment'), and called for the implementation of a Global Taxonomy Initiative (GTI) under the Convention on Biological Diversity (CBD). At a subsequent meeting of the Conference of the Parties (COP4) to the Convention on Biological Diversity in Bratislava, both *The Darwin Declaration* and the implementation of the GTI were accepted. The role of ABRS in supporting and sponsoring taxonomy has thus expanded from a purely national focus, to consideration of the place of Australian taxonomy in a global context.

Chronological list of ABRS publications in botany

1976

Hewson, H.J., *The Family Brassicaceae in Australia*. Herbarium Australiense/Australian Academy of Science, Canberra. [158 pp.]

1978

Burbidge, N.T. (ed. A.McCusker), *Plant Taxonomic Literature in Australian Libraries*. CSIRO/Australian Biological Resources Study, Canberra. [520 pp.]

1979

Chapman, A.D., *Australian Plant Name Index. Abarema–Acacia*. Australian Biological Resources Study, Canberra. [156 pp.; March 1979. An earlier 36-page draft covering *Abbottia* to *Akania* (excl. *Acacia*) was published by the Australian Academy of Science in July 1976]

1980

George, A.S. (ed.), *Flora of Australia Volume 1, Introduction*. Australian Government Publishing Service, Canberra. [x, 200 pp.; 22 August 1981; reprinted 1993]

Anonymous, *Directory of Australian Taxonomists*. Bureau of Flora & Fauna, Canberra. [56 pp.]

1982

George, A.S. (ed.), *Flora of Australia Volume 29, Solanaceae*. Australian Government Publishing Service, Canberra. [vii, 208 pp.; 27 July 1982]

George, A.S. (ed.), *Flora of Australia Volume 8, Lecythidales to Batales*. Australian Government Publishing Service, Canberra. [xii, 420 pp.; 9 December 1982]

1983

Anonymous, *Guide to Collecting Requirements for Australian Flora and Fauna*. Bureau of Flora & Fauna/Australian Government Publishing Service, Canberra. [11 pp.]

1984

Busby, J.R., *Nothofagus cunninghamii* (Southern Beech) Vegetation in Australia. *Australian Flora and Fauna Series No. 1*. Australian Government Publishing Service, Canberra. [69 pp.; July 1984]

George, A.S. (ed.), *Flora of Australia Volume 22, Rhizophorales to Celastrales*. Australian Government Publishing Service, Canberra. [x, 239 pp.; 17 May 1984]

George, A.S. (ed.), *Flora of Australia Volume 4, Phytolaccaceae to Chenopodiaceae*. Australian Government Publishing Service, Canberra. [x, 354 pp.; 12 November 1984]

Anonymous, *Flora of Australia Guide for Contributors*. ABRS, Canberra. (rev. edns 1987, 1993). [26 pp., 1984]

1985

Scott, G.A.M., Southern Australian Liverworts. *Australian Flora and Fauna Series No. 2*. Australian Government Publishing Service, Canberra. [ix, 216 pp.; March 1985; reprinted 1986]

Gill, A.M., Belbin, L. & Chippendale, G.M., Phytogeography of *Eucalyptus* in Australia. *Australian Flora and Fauna Series No. 3*. Australian Government Publishing Service, Canberra. [53 pp.; March 1985; reprinted 1986]

George, A.S. (ed.), *Flora of Australia Volume 25, Melianthaceae to Simaroubaceae*. Australian Government Publishing Service, Canberra. [xii, 215 pp.; 25 December 1985]

1986

Dunlop, C.R. & Bowman, D.M.J.S., Atlas of the Vascular Plant Genera of the Northern Territory. *Australian Flora and Fauna Series No. 6*. Australian Government Publishing Service, Canberra. [116 pp.; c. February 1986]

George, A.S. (ed.), *Flora of Australia Volume 46, Iridaceae to Dioscoreaceae*. Australian Government Publishing Service, Canberra. [xii, 247 pp.; 2 May 1986]

Filson, R.B., Index to Type Specimens of Australian Lichens: 1800–1984. *Australian Flora and Fauna Series No. 4*. Australian Government Publishing Service, Canberra. [iii, 317 pp.; June 1986]

Busby, J.R. & Bridgewater, P.B., A Preliminary Atlas of Mangrove Species in Australia. *Australian Flora and Fauna Series No. 5*. Australian Government Publishing Service, Canberra. [38 pp.; June 1986]

Anonymous, *Flora of Australia Guide for Illustrators*. ABRS, Canberra. (Reprinted 1986; revised edn 1995). [17 pp., 1988]

Anonymous, *Guide to Collecting Requirements for Australian Flora and Fauna* (rev. edn). Bureau of Flora & Fauna/Australian Government Publishing Service, Canberra. [13 pp.]

1987

George, A.S. (ed.), *Flora of Australia Volume 45, Hydatellaceae to Liliaceae*. Australian Government Publishing Service, Canberra. [xvi, 521 pp.; 15 May 1987]

Anonymous, *Register of Taxonomists and Biogeographers*. Australian Government Publishing Service, Canberra. [78 pp.; August 1987]

1988

Hewson, H.J., Plant Indumentum. A Handbook of Terminology. *Australian Flora and Fauna Series No. 9*. Australian Government Publishing Service, Canberra. [vii, 27 pp.; March 1988]

Taylor, A. & Hopper, S., The Banksia Atlas. *Australian Flora and Fauna Series No. 8*. Australian Government Publishing Service, Canberra. [xiv, 257 pp.; April 1988, reprinted with amendments 1990]

George, A.S. (ed.), *Flora of Australia Volume 19, Myrtaceae — Eucalyptus, Angophora*. Australian Government Publishing Service, Canberra. [xvi, 524 pp.; 27 June 1988]

1989

George, A.S. (ed.), *Flora of Australia Volume 3, Hamamelidales to Casuarinales*. Australian Government Publishing Service, Canberra. [xvi, 219 pp.; 24 April 1989]

Streimann, H. & Curnow, J., Catalogue of Mosses of Australia and its External Territories. *Australian Flora and Fauna Series No. 10*. Australian Government Publishing Service, Canberra. [479 pp.; 30 June 1989]

1990

George, A.S. (ed.), *Flora of Australia Volume 18, Podostemaceae to Combretaceae*. Australian Government Publishing Service, Canberra. [xvi, 349 pp.; 8 June 1990]

Hnatiuk, R.J., Census of Australian Vascular Plants. *Australian Flora and Fauna Series No. 11*. Australian Government Publishing Service, Canberra. [xvi, 650 pp.; 20 September 1990]

Anonymous, *Flora of Australia Guide for Contributors to the Bryophyte Volumes*. ABRS, Canberra. [23 pp., 1990]

1991

Chapman, A.D., Australian Plant Name Index A–C. *Australian Flora and Fauna Series No. 12*. Australian Government Publishing Service, Canberra. [xxi, 897 pp.; 20 June 1991]

Chapman, A.D., Australian Plant Name Index D–J. *Australian Flora and Fauna Series No. 13*. Australian Government Publishing Service, Canberra. [ix, 812 pp.; 20 June 1991]

Chapman, A.D., Australian Plant Name Index K–P. *Australian Flora and Fauna Series No. 14*. Australian Government Publishing Service, Canberra. [ix, 766 pp.; 20 June 1991]

Chapman, A.D., Australian Plant Name Index Q–Z. *Australian Flora and Fauna Series No. 15*. Australian Government Publishing Service, Canberra. [ix, 580 pp.; 20 June 1991]

1992

George, A.S. (ed.), *Flora of Australia Volume 35, Brunoniaceae, Goodeniaceae*. Australian Government Publishing Service, Canberra. [xviii, 351 pp.; 6 August 1992]

George, A.S. (ed.), *Flora of Australia Volume 54, Lichens—Introduction, Lecanorales 1*. Australian Government Publishing Service, Canberra. [xviii, 349 pp.; 4 September 1992]

1993

George, A.S., Orchard, A.E. & Hewson, H.J. (eds.) *Flora of Australia Volume 50, Oceanic Islands 2*. Australian Government Publishing Service, Canberra. [xvi, 606 pp.; 29 July 1993]

1994

Womersley, H.B.S., The Marine Benthic Flora of Southern Australia. Rhodophyta – Part IIIA, Bangiophyceae and Florideophyceae (Acrochaetiales, Nemaliales, Gelidiales, Hildenbrandiales and Gigartinales *sensu lato*). *Flora of Australia Supplementary Series No. 1*. Australian Biological Resources Study, Canberra. [508 pp.; 14 Jan. 1994]

Orchard, A.E. (ed.), *Flora of Australia Volume 49, Oceanic Islands 1*. Australian Government Publishing Service, Canberra. [xxiii, 681 pp.; 3 May 1994]

Ramsay, H.P. & Seur, J., Register of Type Specimens of Mosses in Australian Herbaria. *Flora of Australia Supplementary Series No. 2*. Australian Biological Resources Study, Canberra. [142 pp.; 6 July 1994]

Liddle, D.T., Russell-Smith, J., Brock, J., Leach, G.J. & Connors, G.T., Atlas of the Vascular Rainforest Plants of the Northern Territory. *Flora of Australia Supplementary Series No. 3*. Australian Biological Resources Study, Canberra. [164 pp.; 17 November 1994]

Orchard, A.E. (ed.), *Flora of Australia Volume 55, Lichens—Lecanorales 2, Parmeliaceae*. ABRS/CSIRO Publishing, Melbourne. [xviii, 360 pp.; 21 December 1994]

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Orchard, A.E. (ed.), *Flora of Australia Volume 16, Elaeagnaceae, Proteaceae 1*. ABRS, Canberra/CSIRO Publishing, Melbourne. [xxi, 522 pp.; 30 November 1995]

1996

Orchard, A.E. (ed.), *Flora of Australia Volume 28, Gentianales*. ABRS, Canberra/CSIRO Publishing, Melbourne. [xxi, 335 pp.; 28 June 1996]

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Orchard, A.E. (ed.), *Fungi of Australia Volume 1A, Introduction—Classification*. ABRS/CSIRO Publishing, Melbourne. [xxi, 413 pp.; 9 August 1996]

Christophel, D.I. & Rowett, A.I., Leaf and Cuticle Atlas of Australian Leafy Lauraceae. *Flora of Australia Supplementary Series No. 6*. Australian Biological Resources Study, Canberra. [217 pp.; 16 August 1996]

Orchard, A.E. (ed.), *Fungi of Australia Volume 1B, Introduction—Fungi in the Environment*. ABRS/CSIRO Publishing, Melbourne. [xxiii, 405 pp.; 2 October 1996]

Filson, R.B., Checklist of Australian Lichens and Allied Fungi, *Flora of Australia Supplementary Series No. 7*. Australian Biological Resources Study, Canberra. [204 pp.; 20 December 1996]

1997

Orchard, A.E. (ed.), *Fungi of Australia Volume 2A, Catalogue and Bibliography of Australian Macrofungi 1. Basidiomycota p.p.* ABRS/CSIRO Publishing, Melbourne. [x, 348 pp.; 23 April 1997]

1998

Orchard, A.E. (ed.), *Flora of Australia Volume 12, Mimosaceae (excl. Acacia), Caesalpiniaceae*. ABRS, Canberra/CSIRO Publishing, Melbourne. [xx, 213 pp.; 4 May 1998]

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CLASSIFICATION, PHYLOGENY AND THE *FLORA OF AUSTRALIA*

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Floras and the classification of plants

Floras are works of reference about plants, arranged in systematic categories ('taxa'), of defined geographical areas. Because they vary in the amount of detail included as well as the size and complexity of the area covered, they can differ considerably in size and format. In handbooks and more comprehensive Floras, particular attention is given to the principal means of plant identification, *viz*. keys and comparable descriptions of taxa, largely based on morphological characters. The taxon most commonly recognised, and therefore emphasised in Floras, is the 'species' (i.e. the kind or sort). In works of a critical nature, almost equivalent attention may be given to such infra-specific categories as 'subspecies' and 'varietas' (variety). No doubt this is for the practical reason that the information most frequently required by users is that concerning species and subordinate taxa.

In accordance with general principles of classification, the basic taxonomic categories are grouped into larger units: from many rather narrowly defined ones to fewer more inclusive ones. The arrangement of individual plants and populations into larger categories, on the basis of degrees of similarity and of discontinuity in variation, results in a hierarchical system. The information presented in Floras is arranged in accordance with such a system, because it facilitates comparisons if similar taxa are treated in close proximity. With the advent of phylogenetic systematics (below), it is becoming generally accepted that classifications should wherever possible reflect our understanding of phylogeny.

Not all taxa that may be distinguished above the rank of species are of equal interest. Certain ranks are traditionally given greater prominence than others in floras, sometimes to the complete exclusion of intermediate ones. The next category of practical importance above species is that of genus. Although essentially more arbitrary in concept, genera are often more readily recognised than their constituent taxa. A generic name (always treated as a Latin singular noun although frequently of Greek or other derivation) forms the first part of a binary name which is given to every species. The second part is the so-called 'specific epithet', which is usually an adjective. To denote a subspecies or a variety a third element, usually a second adjective, is added to the name of the relevant species. As a result the very nomenclature of plants reflects a systematic arrangement, at least from the generic level downwards.

The present concepts of genus, species and variety can be traced back to the writings of the Swedish botanist Carl Linné (1707–1778) better known as Linnaeus, although they were adapted and defined, rather than invented, by him. Many of the genera and subordinate taxa recognised by Linnaeus have since been widened or, more often, narrowed in their circumscription, but the great majority have survived to form the core of all subsequent systems of classification. For ranks above that of genus, Linnaeus deliberately used an artificial system of orders and classes based on a minimum of arbitrarily chosen floral characters, such as the number of stamens and pistils (the 'sexual system'). He regarded this as the most practical solution for classifying the avalanche of new plants reaching scientists in his day from remote, newly explored parts of the world.

The influence of the Linnaean system was so great that it largely discouraged the development and use of alternatives for over half a century. As knowledge of the world's flora increased, however, botanists became better equipped to design so-called 'natural systems'. These were based on similarities and differences in as many characters as possible, both vegetative and reproductive. The recognition of 'natural orders' was strongly promoted in the latter part of the 18th Century by some French botanists, of whom Antoine Laurent de Jussieu (1748–1836) was the most influential. One of the very first Floras in which genera were arranged by natural orders was also the first concerned with the Australian region, *viz.* Robert Brown's *Prodromus Florae Novae Hollandiae et Insulae Van-Diemen* (1810). During the 19th Century it became customary to replace the term 'natural order' by the alternative 'familia' (family), first promoted by another Frenchman, Michel Adanson (1727–1806).

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Some families such as Apiaceae (Umbelliferae), Brassicaceae (Cruciferae) and Poaceae (Gramineae) were already recognised as natural groups by some of Linnaeus' predecessors and are, therefore, older than the formal category itself. Family names are of practical use because they can be remembered more easily, being rather fewer in number than their included genera. This advantage, however, is somewhat eroded by the trend to divide large 'traditional' families into more homogeneous but smaller ones, as, for example, in the monocotyledons (Dahlgren *et al.*, 1985; Rudall & Chase, 1996). Attempts to place all genera in appropriate families have not been completely successful, but such problems as still exist will probably be solved eventually by modern methods of research, especially the burgeoning molecular approach (below).

For the last hundred years or so, the term 'ordo' (order) has been used for the rank above family in the hierarchical classification. Traditionally, orders have been given scant attention in most Floras. In other taxonomic literature, however, there has been an upsurge of interest in the grouping of taxa into families and higher ranks within the flowering plants. Among recent systems there is an increasing similarity in the concepts of these higher-level taxa. As a result, orders may eventually take over the role of memory pegs from families.

The next major taxonomic category above order is that of 'classis' (class). The question of which group of taxa constitutes a class could be expected to be a subject of much controversy. In the flowering plants, however, there is a remarkable and long-standing agreement among botanists to recognise only two classes, sometimes regarded as subclasses, *viz.* Liliopsida (=Monocotyledoneae) and Magnoliopsida (=Dicotyledoneae). Flowering plants as a whole, previously also known as Angiospermae, or Anthophyta *s. str.*, are ranked sometimes as a 'subdivisio' (Ehrendorfer, 1971), but more usually as a 'divisio' (division), for which the modern name Magnoliophyta has been introduced (Cronquist *et al.*, 1966). (Since 1993 the alternative name 'phylum' has been permitted instead of 'divisio' at this rank.) This taxon in turn may be placed in subregnum Embryobionta (Cronquist *et al.*, 1966), the next highest category. Embryobionta is perhaps more widely known under the older name Cormophyta. The ultimate rank of 'regnum' (kingdom) traditionally accommodated only two major groups: all plants (Vegetabilia or Plantae *s. lat.*) as opposed to animals (Animalia). More recently there has been a movement towards recognising more than two kingdoms, and sometimes even a higher rank, Domain (see below).

System of classification

Formal names

The primary division of all organisms into plants and animals, as reflected in the traditional partitioning of biology into botany and zoology, is no longer regarded as satisfactory from a theoretical point of view. There is a more fundamental difference between those organisms that lack a distinct cellular nucleus (Prokaryota) and those that possess one (Eukaryota). The former group includes only the Schizophyta or bacteria and Cyanophyta or blue-green algae (=kingdom Monera, Raven *et al.*, 1981), but recent molecular phylogenetic research supports the division of Prokaryota into two 'Domains' (above the rank of kingdom), Archaea and

Table 6. Heirarchy of taxonomic categories: major ones in capitals, the most commonly used intermediate ones in lower case. The example shows the classification of the Golden Wattle. Names from subregnum down to divisio after Cronquist *et al*. (1966), from classis to familia after Cronquist (1981). The name for the subseries was not validly published as Bentham did not assign it to a particular rank at any time.

REGNUM (Kingdom)	*Eukaryota* (Organisms with nucleate cells)
Subregnum	*Embryobionta* (Plants with true stems)
DIVISIO (Division, Phylum)	*Magnoliophyta* (Flowering plants)
Subdivisio	
CLASSIS (Class)	*Magnoliopsida* (Dicotyledons)
Subclassis	*Rosidae*
ORDO (Order)	*Fabales* (Leguminous plants)
Subordo	
FAMILIA (Family)	*Mimosaceae* R.Br. (1814)
Subfamilia	
Tribus (Tribe)	*Acacieae* (Reichb.) Endl. (1841)
Subtribus	
GENUS	*Acacia* Miller (1754)
Subgenus	*Acacia* subg. *Heterophyllum* Vassal (1972)
Sectio (Section)	*Acacia* sect. *Phyllodineae* DC. (1825)
Series	*Acacia* ser. *Uninerves* Benth. (1864)
Subseries	[*Acacia* 'Racemosae' Benth. (1842, 1864)]
SPECIES (Species, kind)	*Acacia pycnantha* Benth. (1842)
Subspecies	
VARIETAS (Variety)	Acacia pycnantha Benth. var.pycnantha (1864)

Bacteria (Margulis, 1992; Truper, 1992; Williams & Embley, 1996). In this scheme, Eukaryota comprise a third Domain. Other modern authors prefer to divide the eukaryote organisms into a number of kingdoms or subkingdoms, some accommodating those traditionally regarded as plants. The Protista *s. lat.* (=Protobionta or Thallophyta) may include the autotrophic Algae (=Phycophyta) as well as the heterotrophic Fungi (=Mycophyta). On the other hand, both Protista *s. str.* and (higher) Fungi are more usually treated as equivalent taxa (kingdoms, Raven *et al*., 1981; Margulis, 1992), possibly of the same rank as the Embryobionta, or plants in the narrow sense. Apart from the Magnoliophyta, the Embryobionta accommodates the following divisions (after Cronquist *et al*., 1966): Bryophyta (mosses and liverworts), Psilophyta (whisk ferns), Lycopodiophyta (=lycophytes or clubmosses), Equisetophyta (=sphenophytes or horsetails), Polypodiophyta (=pterophytes or ferns) and Pinophytina (=gymnosperms). Traditionally, Magnoliophyta and Pinophyta have been treated together as Spermatophyta (=phanerogams or seed plants), whereas Embryobionta, excluding Bryophyta but including Pteridophyta (ferns and fern allies), have been grouped together as Tracheophyta (vascular plants). In many Floras coverage is restricted to the Magnoliophyta or Spermatophyta. The Pteridophyta are often included in smaller floras of temperate regions, but otherwise are usually treated, like Bryophyta and Protobionta, in independent and specialised works.

It was originally intended that the *Flora of Australia* would ultimately cover all plants known to grow naturally in the region, except the bacteria. In 1995 it was decided to institute two new, parallel series, *Fungi of Australia* and *Algae of Australia* to describe those taxa traditionally studied by mycologists and phycologists respectively. This decision, partly pragmatic, partly to accommodate developing ideas on the highest levels of biological classification, means that the *Flora of Australia* will now cover the flowering plants, gymnosperms, ferns, fern allies, bryophytes and lichens (i.e. Embryobionta plus lichens – the latter included because they were already partly published at the time the *Fungi of Australia* series was conceived, not from any phylogenetic consideration).

To illustrate what has been discussed in the preceding paragraphs, the hierarchy of taxonomic terms is presented in Table 6 with appropriate names at each rank for *Acacia pycnantha* Benth. From the family level downwards it is customary to provide the name of the original author(s) ('authority'), often in an abbreviated form, after the taxonomic name. These are often useful, particularly as different authors have sometimes used the same name inadvertently for different taxa at the same level, either as independently coined names ('homonyms') or as a result of misinterpretation ('misapplied names'). A name in brackets indicates an earlier author who may have used the same taxonomic name at a different rank in the hierarchy. In the case of an infra-generic name, the author may have used the second or third element of that name originally in combination with the name of another genus or species respectively.

Common names

Parallel to the system of formal taxonomic nomenclature is an informal system of 'common names'. These names follow little recognisable pattern, but are adopted by many because their anglicised form is thought to be easier to remember and pronounce. Common names can be coined by anyone, and may be constructed on descriptive grounds (e.g. Blue Gum, used for many species of *Eucalyptus*), on ecological grounds (e.g. Cassowary Plum; *Cerbera floribunda*, because cassowaries are thought to eat the plum-like fruit), on a fancied resemblance to plants from other areas, particularly Europe (e.g. Native Laurel, used for *Anopterus glandulosus* (Escalloniaceae) because of a resemblance to Northern Hemisphere True Laurel, *Laurus nobilis* (Lauraceae)), or on a translation of all or part of the Latin name (e.g. Blackwood, used for *Acacia melanoxylon*).

Common names, while superficially appealing, offer little or no predicability (–apple as part of a common name usually means that the fruit is relatively large, firm and fleshy but is applied to true apples (*Malus* spp., Rosaceae), pineapples (*Ananas comosus*, Bromeliaceae), Argyle Apples (*Eucalyptus cinerea*, Myrtaceae) and Kangaroo Apples (*Solanum aviculare*, Solanaceae), among very many others. On the other hand, while true pineapples are monocotyledons (Bromeliaceae), as are Pineapple Lilies (*Eucomis* spp., Hyacinthaceae), Pineapple Guava (*Acca sellowiana*) belongs in Myrtaceae, Pineapple Sage (*Salvia elegans*) in Lamiaceae, and Pineapple Weed (*Matricaria discoidea*) in Asteraceae.

Most common names are more or less localised in their application, with the same species called by different common names in different areas. For example, *Hicksbeachia pinnatifida* is variously known as Monkey Nut, Red Bopple Nut, Red Nut, Beef Nut and Red Apple Nut. Alternatively the same common name is applied to a range of different species: Blue Gum is used for numerous *Eucalyptus* species, including *E. globulus, E. saligna, E. tereticornis* and *E. leucoxylon.*

Even the claim that Latin names are hard to pronounce and remember is difficult to defend, given that many Latin names have been adopted as 'common names'. Examples in the Australian flora include *Acacia*, *Banksia*, *Eucalyptus*, *Geranium*, *Goodenia, Grevillea, Hakea* and even *Lechenaultia*. In the cultivated flora the list is even longer, and includes *Amaryllis*, *Daphne*, *Forsythia*, *Fuchsia*, *Gladiolus*, *Lilium*, *Liquidamber*, *Magnolia*, *Pelargonium, Petunia* and many others.

Despite the almost complete lack of rigour in application of common names, they have in some cases attained considerable currency. So that this kind of usage can be tied to more formal usage, in this *Flora* the policy has been to include a limited number of well-established common names, where these are available. It has not been editorial policy to be exhaustive in the search for such names, and it is certainly not editorial policy to encourage the pointless invention of 'common names' known to no-one but the inventor. Where included, common names are capitalised where they apply to a particular species (e.g. Blue Gum), but not capitalised where used as generic descriptors (e.g. eucalypts).

The background to phylogenetic classification

When de Jussieu proposed a natural system for the classification of plants in his *Genera Plantarum* (Jussieu, 1789), he probably did so as a true representative of the so-called 'idealistic morphologists'. It is unlikely that he considered the distinguishing characters of the respective groups of plants to be the result of an evolutionary process, as such hypotheses hardly entered scientific thought until the end of the 18th Century. Contemporary biologists saw it as their task to recognise the essential (or 'archetypal') characters of taxa, thought to be obscured in Nature by a multitude of variants (Stevens, 1984). They believed that a natural system of classification of all creatures (and plants) should reflect the 'Grand Design' (in a theological or philosophical sense) fundamental to Nature.

The first theory to challenge the idea of immutability of species with some success was proposed by the Parisian professor Jean Monnet de Lamarck in his *Philosophie Zoologique* (Lamarck, 1809). It was Charles Darwin's *On the Origin of Species by Means of Natural Selection* (Darwin, 1859), however, that profoundly changed biological and philosophical thinking. Natural systems acquired a new dimension through evolutionary theories, and were increasingly regarded as models reflecting degrees of actual relationship through common descent. Species within a single genus were considered to have diverged from each other later or more slowly (and therefore to a lesser degree) than genera within a family. The same principle was believed to apply to other taxonomic ranks. A stepped hierarchical system cannot, however, adequately reflect all stages of gradual diversification at any one time. Therefore, a decision to recognise a particular group as a distinct taxon at a particular rank will always be somewhat arbitrary. In certain groups, taxa at the species level may be clearly isolated from each other by discontinuities in character variation, whereas taxa of higher rank may be difficult to segregate and circumscribe (e.g. Asteraceae – *Cassinia/Ozothamnus*, Brassicaceae – many genera). On the other hand, certain genera may be easy to define and agree upon, but their subdivision into species may be difficult because natural populations show overlapping ranges of variation in a number of characters (e.g. *Eucalyptus s. str.*). Such difficulties may well be manifested in Floras through keys to identification that do not always give satisfactory results.

Darwin's ideas undoubtedly had an impact on the natural system of plant classification developed by George Bentham and Joseph Hooker. Published in their *Genera Plantarum* (Bentham & Hooker, 1862–1883), this system was most influential until the beginning of the 20th Century. It is interesting to note that the only comprehensive flora yet completed for the Australian region as a whole, Bentham's *Flora Australiensis* (Bentham, 1863–1878), was one of the first great Floras written in that period.

From the beginning of the 20th Century, genetic research provided a deeper insight into the nature of morphologically-based taxa, particularly at generic and subordinate levels. It has become clear that it is not particularly useful to recognise formal categories at very low levels, such as subvarieties, forms and even subforms, as was fashionable in some 'schools' until quite recently. On the other hand, varieties and higher taxa, originally only recognised because of apparent similarities of the constituent individuals ('phenotypes'), have usually been shown to have a common genetic potential ('gene pool'). Encouraged by these results, botanists have attempted to provide definitions for the lower taxa, in particular the species, by using more objective criteria, e.g. the degree of fertility between individuals or populations. They have, however, failed to find any criteria that are suitable for universal application and it seems as yet impossible to remove subjectivity from taxonomic practice.

For practical reasons, most plant taxa are still recognised and defined primarily by gross morphological characters ('alpha taxonomy'). It is possible nowadays to test similarities and discontinuities by using additional criteria derived from such disciplines as anatomy (Metcalfe, 1960–1995; Huber 1969; Stebbins, 1975; Corner, 1976; Metcalfe & Chalk, 1979–1987; Gifford & Foster, 1989; Claugher, 1990), palynology (Erdtman, 1966, 1969; Walker, 1976), embryology (Davis, 1966; Dahlgren, 1975b), cytology and genetics (Stebbins, 1971; Jackson, 1976; James, 1981; Briggs & Walters, 1984; Kellogg, 1989; Seberg, 1989; Stace, 1989), phytochemistry (Hegnauer, 1962–1973; Bendz & Santesson, 1973; Gibbs, 1974; Jensen *et al.*, 1975; Cronquist, 1977; Gornall *et al.*, 1979; Bisby *et al.*, 1980; Dahlgren, 1981; Harborne & Turner, 1984), and even parasitology (Hedberg, 1979). Incorporation of this additional information from a wide range of disciplines is sometimes known as 'omega taxonomy'. Taxonomists usually take into account significant results from these areas of research when circumscribing taxa and designing systems of classification. However, it may be argued that if all taxonomic studies were made on such a comprehensive scale, it would slow down a more balanced accumulation of taxonomic knowledge over the widest possible front. In the face of accelerating threats to the natural environment, some authors suggest that documentation of biological diversity at the most basic, descriptive level is urgently needed, especially given the increasing shortage of taxonomists (Arroyo *et al.*, 1992; Gaston & May, 1992; Wilson, 1992; Gaston & Mound, 1993; Visher, 1996). On the other hand, many authors argue that documentation is of limited value without the deeper insights gained from monographic and phylogenetic studies (Stork & Gaston, 1990; Brooks *et al.*, 1992; Anonymous, 1994; Linder & Midgley, 1994; Renner & Ricklefs, 1994). The *Flora of Australia* project, as part of the wider Australian Biological Resources Study, is adopting a compromise approach, producing a full account of what is currently known of the Australian flora, while supporting in-depth study of some of the more complex issues through taxonomic research under the Participatory Program.

Phylogenetic methods

In recent decades, two developments have been changing the way systematists work, and are providing answers to long-standing problems in classification, especially at higher taxonomic levels. These are cladistics and techniques for rapidly amplifying and sequencing DNA.

Cladistic theory, based on the ideas of Hennig (1950, 1966), has assumed a major role in taxonomic botany, particularly at the levels of genus and above. More recent introductions are given by Crisp & Weston (1987), Linder (1988), Forey *et al.* (1992), Smith (1994), and Morrison (1997). Hennigian theory considers a group monophyletic (and thus taxonomically sound) only if it includes all of the descendants of the most recent common ancestor. In constructing cladistic trees (cladograms), the character states of the constituent taxa are polarised, i.e. the direction of derivation of character states is established by comparison with their closest relation (sister group) or several closely related groups (outgroups). Some states are polarised as ancestral (plesiomorphic) and others as derived (apomorphic) within the group. Taxa may share derived character states (synapomorphies), and can be grouped on this basis at various levels. Shared primitive states (symplesiomorphies) are considered uninformative and are not used for grouping. Conflict among characters implies homoplasy (parallelisms and reversals) and results in multiple different cladograms. Therefore, the most parsimonious solutions (i.e. those that offer the fewest parallelisms and reversals) are sought as the most likely reflection of phylogeny. Ideally, the cladogram will be fully resolved, with all branches dichotomous, but no characters may be available to resolve some branches. Also, if homoplasy results in many equally parsimonious trees, then a partly resolved consensus tree may be presented, showing only those branches that are contained in all or a majority of the most parsimonious trees.

Difficulties with phylogenetic reconstruction

Hennigian methodology has been slow to gain acceptance, and is still resisted in some quarters. For instance, Lamboy (1994, 1996), using simulations, claimed that cladistic analysis using morphological data was likely to fail to find the 'true' phylogeny in most cases. Wiens & Hillis (1996), on the other hand, claimed Lamboy's simulation method to be flawed. Criticisms have been levelled at almost every aspect of cladistic methodology, and these are too numerous to review here. Many are discussed in the introductory references given above (see, in particular, Cronquist, 1987). Most criticisms have been rebutted and phylogenetic analysis is widely practised as the basis for classification. This is not to say that cladistics is without problems – on the contrary. Some of the main difficulties and how they are being dealt with are discussed briefly below.

True phylogeny unknowable

Since the evolutionary history of organisms is unique and can never be revisited, the true phylogeny of organisms can never be known. No matter how good our methods of reconstructing it, the best phylogeny will always be an hypothesis, subject to falsification. This is true of any putatively natural classification, whether derived from an estimate of phylogeny or by some other method.

Reticulation

Hybridisation is relatively common among plants, not only between species and infraspecific groups, but on occasion at higher levels as well (e.g. it is well known that wide-ranging intergeneric hybrids are possible in Orchidaceae, and taxa are apparently maintained by specialist pollination techniques involving specific insects; see, for example, Bower, 1996). This leads to a reticulate pattern of evolution in many groups, and is contrary to Hennigian theory, which assumes evolution to be dichotomous and non-reticulate.

In most Australian groups some degree of inter-specific hybridisation occurs (Clifford, 1963), and is mentioned in the *Flora of Australia* accounts. Many of these hybrids are ephemeral, and have little potential impact on macro-evolution of the group. In other cases they can lead to major hybrid swarms which may be numerically more common than the parental species. These swarms have the potential to develop into one or more stable descendant taxa given sufficient time (e.g. *Bedfordia*; Orchard, unpubl. data).

In some cases polyploid complexes develop, either within a species (autopolyploidy), or subsequent to hybridisation (allopolyploidy). In the latter case, the polyploid (e.g. tetraploid, hexaploid, octoploid etc.) derivative taxa are usually genetically isolated from their diploid parents, and often are morphologically distinct as well. Examples in the Australian flora include *Allocasuarina*, *Dampiera*, *Danthonia s. lat.*, *Rubus*, *Rumex*, *Senna*, *Taraxacum* and many ferns. *Senna* is a particularly interesting case, where hybridisation, polyploidy and apomixis have all been involved in the evolutionary development of the current taxa (see *Flora of Australia* Vol. 12; Randell, 1988, 1989, 1990). This suggests that, in these taxa at least, evolution is reticulate, not tree-like as assumed by cladistic methods. If reticulate evolution were the norm, then using branching trees to model it would be falsified. Even if evolution is predominantly tree-like but occasionally reticulate (undoubtedly the case), phylogenetic reconstruction is confounded in particular instances.

Whether the history of life is predominently tree-like may be examined by statistical tests such as the permutation tail probability test (Faith & Cranston, 1991), which asks whether the cladistic structure in a data set occurs by chance. Currently there is active research towards developing tests of the reliability of estimates of phylogeny (Penny *et al.*, 1992; Hillis, 1995; Huelsenbeck, 1995). Moreover, a tree obtained with one data set (e.g. morphological) may be tested by an independent data set (e.g. DNA sequences). These tests do not falsify the assumption of an underlying tree in most cases. Previous high estimates of the rate of hybrid speciation based on the frequency of polyploidy (Grant, 1971) were probably biased by ignoring the vertical inheritance of a polyploid set of chromosomes from an ancestor (McDade, 1995). Various methods have been proposed for detecting hybrid speciation in individual cases, and taking this into account when reconstructing phylogeny (Funk, 1985; McDade, 1995). One approach constructs trees that are partly branching, partly reticulate (Alroy, 1995).

Abundant homoplasy

It has been suggested frequently that too much convergent evolution (independent evolution of the 'same' feature in different lineages) would confound phylogenetic reconstruction even if evolutionary history is tree-like. For example, Linnaeus' sexual system of classification is known to be false, due to the repeated evolution of the same numbers of various floral parts in obviously unrelated plant families (Linnaeus himself recognised this, and never claimed that his system was other than a pragmatic classification of convenience). However, Farris (1983) showed the power of parsimony to extract the phylogenetic 'signal' from homoplasious 'noise', even when the latter is far more abundant. Moreover, the statistical methods mentioned in the previous section can test the robustness of a phylogenetic estimate in the presence of homoplasy. A particular version of this problem occurs when analysing DNA sequences, because only four states of each character are possible (A, G, C and T). This leads to compounded convergence ('multiple hits') over long evolutionary periods. Methods have been developed to correct for this problem using maximum likelihood analysis.

Inadequate fossil record

Since publication of the *Origin of Species* (Darwin, 1859) it has been thought that the fossil record provides the key (if not the only) means of reconstructing evolutionary history (for a relatively modern espousal of this view see Sporne, 1976). However, Darwin and most subsequent workers have been well aware of the deficiencies of the fossil record, mainly because of its many gaps. Although it is relatively good for some categories of organisms (mostly animal groups such as molluscs and vertebrates), it is rather poor for others, particularly many plant groups. Consequently, fossil evidence for evolutionary history is largely lacking in a group such as the flowering plants and may never become available. Phylogenetic reconstruction must therefore be based mainly on evidence derived from living representatives.

Part of this traditional view is that the fossil record provides direct evidence for evolutionary history in the sense that fossils represent extinct ancestors. However, Patterson (1977) pointed out that the fossil record does not, in fact cannot, give direct evidence for the pathway of evolution (and neither can living organisms). Fossils can demonstrate that certain organisms did in fact exist, but cannot prove that they were actually ancestral to others. Phylogenetic reconstruction can only produce a hypothetical evolutionary tree in which all observed organisms, both extant and fossil, are at the tips of the branches. Thus the trees produced by some workers in which all the key positions of the branching system are occupied by either recent or fossil taxa should be regarded as pseudo-phylogenetic (Patterson, 1997; Stevens, 1984).

This is not to say that fossils have no part to play in elucidating phylogeny. On the contrary, fossil data are invaluable (if not essential) and should be incorporated together with data from contemporary organisms into cladistic analyses (Smith, 1994). For example, there has been a recent surge of interest in land plant evolution, stimulated by cladistic analyses incorporating new palaeobotanical discoveries and new data from living plants, both molecular and morphological (Kenrick & Crane, 1997a, 1997b).

The impact of molecular data

When the first edition of this volume was published in 1981, use of molecular data to investigate phylogeny was restricted to a handful of laboratories around the world. It was slow, expensive and seemed irrelevant to the everyday practice of taxonomy. Since then, the polymerase chain reaction (PCR) has been developed, and the methods have become so much quicker and cheaper that they are impinging on taxonomy at every level (Crawford, 1990; Soltis *et al.*, 1992; Hillis *et al.*, 1996). Our understanding of higher level taxa has been most affected, especially within angiosperms and among their seed plant relatives. High level classification has traditionally been the most problematic (except for recognition of some very distinctive groups such as angiosperms and monocotyledons), because the morphological characters used, mainly floral, are rife with convergence.

Sequences of the chloroplast gene for rubisco (*rbc*L) and that for 18S ribosomal RNA provide the largest data sets. The rapidity with which these data are accumulating is demonstrated by the case of *rbc*L. A phylogeny of seed plant relationships published in 1993 (Chase *et al.*, 1993) included sequences for 499 species. Only three years later, an analysis was presented with more than 2500 sequences (Kallersjo, 1996). A number of important analyses above family level have been published already (Olmstead *et al.*, 1992; Chase *et al.*, 1993; Savard *et al.*, 1994; Duvall *et al.*, 1995; Nickrent & Soltis, 1995; Gustaffson *et al.*, 1996; Hershkovitz & Zimmer, 1996), as well as several which integrate morphological and molecular data in a single analysis (Doyle *et al.*, 1994; Drinnan *et al.*, 1994; Olmstead & Sweere, 1994; Pryer *et al.*, 1995). Monophyly is supported for important groups such as seed plants, anthophytes (angiosperms + Gnetales), angiosperms, monocotyledons, eudicotyledons ('true dicotyledons', ie excluding some 'primitive' groups – see below), and two major groups within eudicotyledons, rosids and asterids (Chase *et al.*, 1993; Bremer *et al.*, 1996). Others such as seed ferns, dicotyledons *s. lat.* and Magnoliidae are not supported. Both morphological and molecular data have shown several families to be nested within others, e.g. Apiaceae within Araliaceae (Judd *et al.*, 1994; Plunkett *et al.*, 1996), Epacridaceae within Ericaceae (Kron & Chase, 1993), and Baueraceae and Eucryphiaceae within Cunoniaceae (Hufford & Dickison, 1992). However, many major problems remain, such as the basal branching of the angiosperm phylogeny, and interrelationships of the major seed plant groups. This research is still in its early stages, but already it is becoming routine for monographic studies to include DNA sequencing.

Does the molecular revolution threaten traditional morphology research using morphology and herbarium specimens? On the contrary, molecular phylogenies are rejuvenating morphological research by suggesting the most informative characters, and by helping to reinterpret others. For example, a large clade comprising most (but not all) dicotyledons is strongly supported by molecular data sets. This group has not been recognised before, and is informally known as the eudicotyledons. It excludes monocotyledons and 'primitive' dicotyledons such as Magnoliales, Laurales, Piperales and Nymphaeaceae (Bremer's tree). Interestingly, eudicotyledons share the advanced morphological character state of triaperturate pollen, the significance of which was not appreciated until molecular analyses identified the eudicotyledons.

Should classification be phylogenetic or pragmatic?

From a phylogenetic point of view, the ultimate aim of classification must surely be to reflect the 'tree of life' as faithfully as possible. Such a classification should be at once the most stable and the most predictive (assuming there is only one tree of life). There are some problems in achieving this. First, no phylogenetic analysis has been made for many taxonomic groups. This problem will disappear in time, as cladistic analyses proceed for more and more groups. Second, an estimate of phylogeny may differ considerably from the traditional classification, requiring many changes to nomenclature. This problem is more serious at the lowest taxonomic levels, due to the binomial and trinomial system of nomenclature there, but also occurs at higher levels when taxa are shown to be non-monophyletic.

Classifications and their attendant nomenclature also have a utilitarian facet, and in fact this was their original function. While a pragmatic, utilitarian classification may be identical with a phylogenetic one, it is not necessarily so. For example, for many purposes it may be convenient to recognise 'eucalypts' as distinct from *Angophora*, while from a strictly phylogenetic point of view, if one recognises *Angophora*, then one should also distinguish between *Eucalyptus s. str*. and *Corymbia* (Udovicic *et al*., 1995; Ladiges *et al*., 1995; Hill & Johnson, 1995). Changes to classification and nomenclature are very disruptive to users of taxonomy, including legislators, horticulturalists, ecologists and others. For this reason, an existing classification should only be overturned when the competing phylogeny is shown to be well-corroborated, by statistical testing as well as by multiple lines of evidence. For instance, the eucalypts were only split into two genera after morphology and two different molecular data sets agreed that bloodwoods (*Corymbia*) were more closely related to *Angophora* than to *Eucalyptus s. str*.

These problems lead in some cases to the adoption of a pragmatic and more conservative classification for everyday purposes, such as Floras. A problem arises when taxa recognised in these classifications are paraphyletic, and are used for biological applications. Paraphyletic taxa, such as 'gymnosperms' and 'dicotyledons' are defended by some authors (Cronquist, 1987; Brummitt, 1996), but should not be used in evolutionary biology, since they are not evolutionary units (Donoghue & Cantino, 1988; Humphries & Chappill, 1988). If non-phylogenetic taxa are used for evolutionary applications (as is often done), then serious error will result (Donoghue, 1989; Funk, 1993).

A schematic presentation of a modern phylogenetic system of classification of the Magnoliophyta by the Swedish taxonomist Rolf Dahlgren (1980) is reproduced in Fig. 29. In this diagram, the 'tips of the branches' have been grouped into larger units (orders and superorders) by cladistic methods. Their relative proximity is an expression of similarity or dissimilarity in a range of characters. A very good recent introduction to the phylogeny of angiosperms is Bremer *et al*. (1996). Their tree is reproduced in Fig. 30.

The system used in the *Flora of Australia*

As explained above, the nomenclature of plants itself imposes on Floras a systematic grouping from the generic level down, but a particular classification system must be adopted for the placement of genera into families. The choice of a system does not necessarily determine the sequence of genera and families, since these may be arranged alphabetically or according to assumed relationships at any or all of these levels. A sequence according to degrees of similarity appears preferable, particularly in works which deal with many representatives of any one taxon. Taxonomic relationships would be best expressed in a multi-dimensional scheme, whereas the treatment in a book necessarily follows a more arbitrary linear sequence. In practice this does not appear to be a major disadvantage. It could also be argued that any systematic arrangement of taxa in a Flora is primarily an expediency, theoretical considerations being of little interest to most users. Nevertheless, it is undesirable to choose a system that is clearly out of date.

The Editorial Committee for the *Flora of Australia* decided in 1979 that a sequential system should be adopted, so that the families could be assigned to particular volumes from the beginning. For the flowering plants their choice fell on the latest version of Arthur Cronquist's system then being prepared for publication (Cronquist, 1981), since it was thought that it would be the most modern published by the time the first volumes of the *Flora* were to appear. Cronquist's system, as relevant to Australia, is given on the front endpapers of this introductory volume, together with a schedule for the Flora. A systematic arrangement of taxa other than Magnoliophyta has been decided subsequently, and appears at the beginning of each major section of the series (Volume 48 for the ferns and gymnosperms, Volume 51 for the Bryophytes, Volume 54 for the lichens, *Fungi of Australia* Volume 1A for the fungi *s. lat*.).

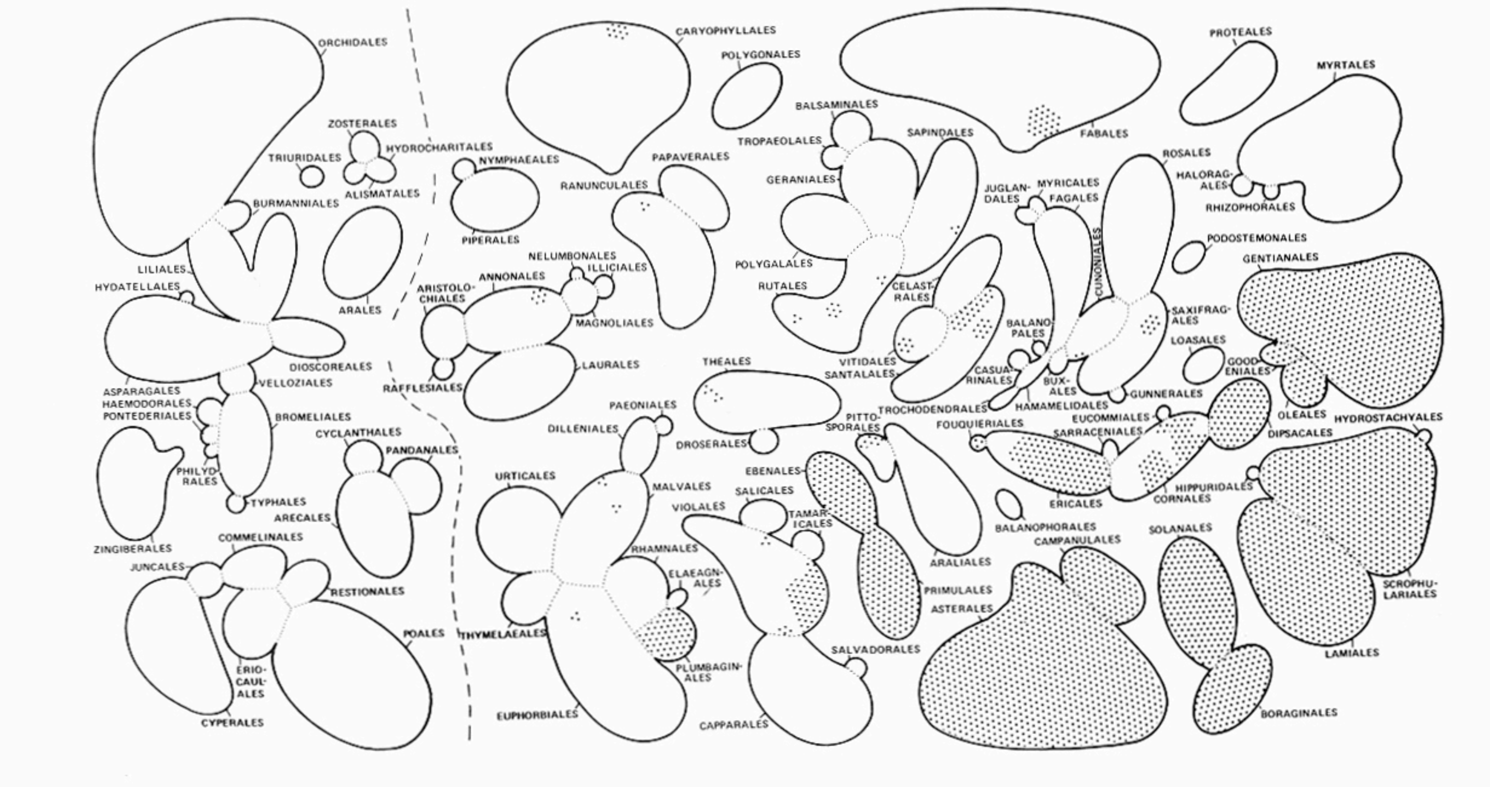

Figure 29. The orders of the *Magnoliophyta* (Flowering Plants), shown as clusters of superorders. The broken line separates the classes *Liliopsida* (Monocotyledons) on the left and *Magnoliopsida* (Dicotyledons) on the right. Shading indicates the occurrence of sympetalous flowers in orders (or parts thereof) of the latter class, showing that taxa similar in this respect may not be closely related. The diagram could be interpreted as a chronological cross-section (the present) through the branching system of an imaginary phylogenetic tree. (After Dahlgren, 1980; reproduced with permission of the author).

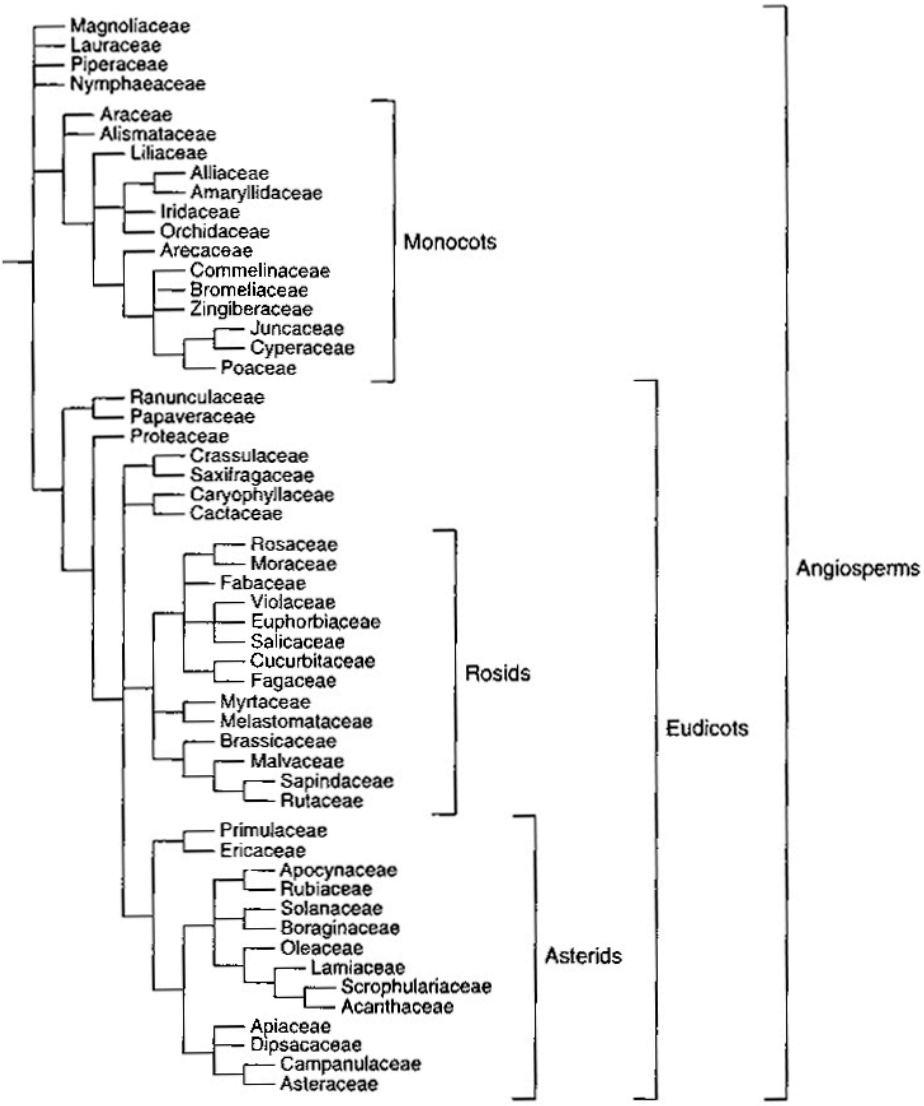

Figure 30. Schematic presentation of a modern phylogenetic system of classification (Reproduced from Bremer, 1996, with permission).

Current systems of Magnoliophyta

In the first edition of this work Andrew Kanis (1981) provided a comparison of the higher level (Orders and Families) classifications adopted by Melchior (1964), Airy Shaw (1973), Hutchinson (1973), Takhtajan (1980), Dahlgren (1980), Thorne (1981) and Cronquist (1981). This is not repeated here. A more recent comparative study of major classifications at the family level and above is given by Brummitt (1992). Since Kanis' survey a number of additional papers have appeared, some of the more important of which are mentioned briefly below.

A comprehensive rearrangement occurred in the monocotyledons in the late 1970s and 1980s. Books and papers by Hamann (1976), Clifford (1977), Dahlgren & Clifford (1982), Dahlgren & Rasmussen (1983) and Dahlgren, Clifford & Yeo (1985) recognised many segregate families, particularly within the old Liliaceae/Iridaceae/Amaryllidaceae complex. In describing these taxa the *Flora of Australia* (Vols 45, 46) has retained the Cronquist family delimitations, but has provided tables of equivalents for the Dahlgren *et al.* classification, under Liliaceae (*Flora of Australia* Vol. 45: 149–151) and Xanthorrhoeaceae (*Flora of Australia* Vol. 45: 88–89). Dahlgren also continued to modify his views on the dicotyledons, and presented a new overview of his system in 1983 (Dahlgren, 1983).

A new version of the Thorne systems appeared in 1983 (Thorne, 1983). Takhtajan published an update of his views on angiosperm origins in 1987 (Takhtajan, 1987a), a new version of his classification in 1987, in Russian (Takhtajan, 1987b), and an English version of his revised classification in 1997 (Takhtajan, 1997). In the last he gave a further brief synopsis of his views on evolution and phylogeny, with descriptions of families, orders and higher level taxa.

Cronquist presented a new edition of his scheme in 1988 (Cronquist, 1988). This differed only in minor respects from his 1981 classification. Among new elements of particular significance to the Australian flora was recognition of Nothofagaceae as distinct from Fagaceae (although still adjacent to it). To minimise confusion, the *Flora of Australia* has continued to follow Cronquist (1981) in respect to family delimitation. However, in those cases where authors believe that evidence supports other taxonomies they are encouraged to provide brief notes outlining these alternative views as part of family or generic descriptions, as appropriate. Thus while Cronquist (1981) continues to provide the pragmatic skeleton on which the *Flora of Australia* is hung, it is not advanced as necessarily the best or only scheme, especially from a strictly phylogenetic point of view.

A very useful multi-author overview of Australian flowering plant families was produced by Morley & Toelken (1983), modelled on the very successful *Flowering Plants of the World* (Heywood, 1978). It is based on the classification scheme of Takhtajan (1969). The *Dictionary of the Flowering Plants and Ferns* of Willis and Airy Shaw was remodelled and updated in a new format by Mabberley (1987, 1997) and remains probably the best concise encyclopaedia of information on world vascular plant genera and families.

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ANNOTATED BIBLIOGRAPHY

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The following bibliography lists, in chronological order, the most significant floristic works that have been written for Australia and major regions within it. Several early general taxonomic works of relevance are also included. Some recent major works peripheral to taxonomy (e.g. horticulture, endangered species, poisonous plants) are also listed. Publication years differing from those on title-pages are given in square brackets.

Monographic works on a particular family or genus are not included here. They will be listed under the relevant taxon in *Flora of Australia* Volumes 2–59.

18th Century

Burman, N.L. (1768), *Flora Indica*. Haak, Leiden & Schreuder, Amsterdam.

Contains the first two Australian plants named under the Linnaean system, both described as ferns attributed to Java, but in fact species of *Acacia* (*A. truncata* (Burm.f.) Hoffmanns. – Mimosaceae) and *Synaphea* (*S. spinulosa* (Burm.f.) Merr. – Proteaceae) from south-western Australia.

Linnaeus, C. (fil.) (1782), *Supplementum Plantarum Systematis Vegetabilium, Generum Plantarum, et Specierum Plantarum*. Impensis Orphanotrophei, Braunschweig.

Contains descriptions of several Australian plants seen by Linnaeus in Banks' herbarium.

Cavanilles, A.J. (1791–1801), *Icones et Descriptiones Plantarum, quae aut Sponte in Hispania Crescunt, aut in Hortis Hospitantur*. Typographia Regia, Madrid.

Includes descriptions of plants from Port Jackson and Botany Bay, collected by Luis Née, a member of the Spanish Malaspina expedition to the South Seas. Amongst other taxa, the genera *Angophora* and *Bursaria* were described in this work (both in 1797*)*. See also Cavanilles (1800).

Smith, J.E. (1793)[–1795], *A Specimen of the Botany of New Holland*. Davis, London.

Descriptions of plants collected at Sydney by early settlers, chiefly John White.

1800–1850

Cavanilles, A.J. (1800), Observaciones sobre el suelo, naturales y plantas del Puerto Jackson y Bahía-Botánica, *Anales de Historia Natural* 1, 3: 181–245.

Descriptions of the plants collected at Sydney in March–April 1793 by Luis Née, a member of the Spanish Malaspina expedition to the South Seas.

Labillardière, J.J.H. de (1804–1806)[–1807], *Novae Hollandiae Plantarum Specimen*, 2 vols. Huzard, Paris.

Descriptions of plants collected by Labillardière and others in south-western Australia and Tasmania in 1792–1793, arranged in the Linnaean system.

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[1] Australian Biological Resources Study, GPO Box 636, Canberra, Australian Capital Territory 2601.

[2] 'Four Gables', 18 Barclay Rd, Kardinya, Western Australia 6163.

Brown, R. (1810), *Prodromus Florae Novae Hollandiae et Insulae Van-Diemen*. Taylor, London.

The first Flora of Australia, albeit incomplete, based largely on the extensive collections made by Brown himself during the Flinders *Investigator* voyage (1801–1803) and afterwards in New South Wales and Tasmania. Only one of two projected volumes published. One of the first major works to be based on a natural system.

Candolle, A.P. de (*et al.*) [1824–](1823–1873), *Prodromus Systematis Naturalis Regni Vegetabilis*. Treuttel & Wurtz, Paris.

One of the greatest botanical works, intended to cover the flowering plants of the world but eventually including only the dicotyledons. The principles of nomenclature used in the work became the basis for the International Code of Botanical Nomenclature.

Endlicher, S.F.L. (1833), *Prodromus Florae Norfolkicae sive Catalogus Stirpium quae in Insula Norfolk Annis 1804 et 1805 a Ferdinando Bauer Collectae et Depictae*... Friedrich Beck, Wien.

First Flora of Norfolk Island, based on the collections and illustrations of Ferdinand Bauer.

Endlicher, S.F.L. (1837), *Enumeratio Plantarum quas in Novae Hollandiae Ora Austro-occidentali ad Fluvium Cygnorum et in Sinu Regis Georgii collegit Carolus Liber Baro de Hügel*. Friedrich Beck, Wien.

Descriptions of Western Australian plants collected near the Swan River settlement and at King George Sound by Baron von Hügel in 1833–1834. See also Endlicher (1838).

Endlicher, S.F.L. (1838), *Stirpium Australasicarum Herbarii Hügeliani Decades Tres*. J.P.Sollinger, Wien.

Descriptions of Western Australian plants collected near the Swan River settlement and at King George Sound by Baron von Hügel in 1833–1834. A preprint with new pagination of an article which also appeared in *Annalen des Wiener Museums der Naturgeschichte* 2: 189–212, 1839. See also Endlicher (1837).

Mitchell, T.L. (1838), *Three Expeditions into the Interior of Eastern Australia*. T. & W.Boone, London.

Contains descriptions by John Lindley of 77 new species from inland Queensland, New South Wales and Victoria.

Lindley, J. (1839–1840), Sketch of the Vegetation of the Swan River Colony, Appendix to the first 23 volumes of *Edwards's Botanical Register*.

Descriptions of the plants collected by early settlers at the Swan River, Western Australia.

Lehmann, [J.G.]C. (1844–1847)[–1848], *Plantae Preissianae sive Enumeratio Plantarum, quas in Australasia Occidentali et Meridionali-occidentali Annis 1838–1841 Collegit Ludovicus Preiss*. Meissner, Hamburg.

Almost a preliminary Flora of south-western Western Australia, but without keys. Volume 2 also included many Drummond collections.

1851–1900

Hooker, J.D. (1855–1860)[–1859], *The Botany of the Antarctic Voyage of H.M. Discovery Ships 'Erebus' and 'Terror', in the Years 1839–1843, under the Command of Captain Sir James Clark Ross, Vol. III, Flora Tasmaniae*. Reeve, London.

The botanical results of the expedition's visit to Tasmania, together with an important essay on the Australian flora. The descriptions were based primarily on Hooker's own collections, supplemented by those received from Gunn, Lawrence and others.

Harvey, W.H. (1858–1863), *Phycologia Australica, or a History of Australian Sea-weeds*, 5 vols. Reeve, London.

Colour plates and descriptions of the first major collections of Australian marine algae.

Mueller, F.J.H. (1858–1882), *Fragmenta Phytographiae Australiae*, Vols I–XII (part I). Joannis Ferres, Government Printer, Melbourne.

A series containing descriptions of many new genera and species, comments on the status and relationships of many taxa, and notes on distribution.

Mueller, F.J.H. [1862–](1860–1865), *The Plants Indigenous to the Colony of Victoria, Vols I, II*. Government Printer, Melbourne.

The first attempt at a State Flora in Australia. Only the first 40 pages of the second volume were published.

Bentham, G. (1863–1878), *Flora Australiensis: a Description of the Plants of the Australian Territory*. Reeve, London.

The standard Australian Flora for over a century; described 8125 species.

Spicer, W.W. (1878), *A Handbook of the Plants of Tasmania*. Walch, Hobart.

A key to species, together with a systematic checklist and brief distributions, compiled by a clergyman. Arranged in the system of *Flora Australiensis*.

Woolls, W. (1880), *Plants Indigenous in the Neighbourhood of Sydney*. Government Printer, Sydney.

A census of flowering plants and ferns with authorities, arranged in Mueller's system.

Tate, R. (1880), A census of the indigenous flowering plants and ferns of extratropical South Australia, *Transactions of the Royal Society of South Australia* 3: 46–90.

A census with references to *Flora Australiensis* or Mueller's *Fragmenta*, and distribution in eight regions of the State. Arranged in Mueller's system. A supplement was issued in *Trans. Roy. Soc. S. Australia* 4: 102–111 (1882).

Mueller, F.J.H. von (1882), *Systematic Census of Australian Plants with Chronologic, Literary and Geographic Annotations. Part I, Vasculares*. Government Printer, Melbourne.

A census arranged in Mueller's own system which was based on Bentham's *Flora Australiensis*, together with original references, distribution by States, and the relevant references to *Flora Australiensis* and Mueller's *Fragmenta*; contains 8646 species.

Bailey, F.M. (1883), *A Synopsis of the Queensland Flora, Containing both the Phanerogamous and Cryptogamous Plants*. Government Printer, Brisbane.

A very concise Flora, without keys, arranged in the Bentham & Hooker system and with a systematic index. Includes the ferns, mosses, lichens, fungi and algae, with family and generic descriptions and lists of species.

Moore, C. (1884), *A Census of the Plants of New South Wales*. Thomas Richards, Sydney.

A list of names and authorities, based principally on the *Census* of Mueller (1882), essentially following the nomenclature and classification of Bentham (1863–1878).

Woolls, W. (1885), *The Plants of New South Wales*. Thomas Richards, Sydney.

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Mueller, F.J.H. von [1886–](1885–1888), *Key to the System of Victorian Plants*, 2 parts. Government Printer, Melbourne.

Part I: A key with very short generic and specific diagnoses; includes a list of aliens.

Part II: A systematic list with distributions and illustrations.

Mueller, F.J.H. von (1889), *Second Systematic Census of Australian Plants, with Chronologic, Literary and Geographic Annotations, Part I, Vasculares*. Government Printer, Melbourne.

A revision of the *Census* of 1882; contains 8839 species.

Tate, R. (1890), *A Handbook of the Flora of Extratropical South Australia, Containing the Flowering Plants and Ferns*. Education Department, Adelaide.

An amplified key, covering a total of 1935 species, together with a list giving distributions. Arranged in the Bentham & Hooker system.

Bailey, F.M. (1892), *Lithograms of the Ferns of Queensland*. Government Engraving & Lithographic Office, Brisbane.

Illustrations only.

Moore, C. & Betche, E. (1893), *Handbook of the Flora of New South Wales*. Government Printer, Sydney.

Keys to families and genera, and amplified keys to species of flowering plants and ferns with brief generic descriptions; based on Mueller's system.

McAlpine, D. (1895), *Systematic Arrangment of Australian Fungi, together with Host-Index and List of Works on the Subject*. Government Printer, Melbourne.

A census with original references, brief diagnoses, and distributions by States; arranged in McAlpine's own system.

Bailey, F.M. (1899–1902), *The Queensland Flora,* 6 vols. Diddams, Brisbane.

Based directly on *Flora Australiensis* with the addition of species described since that work and illustrations of some species. An index was issued in 1905.

1901–1950

Maiden, J.H. [1903–](1902–1925), *The Forest Flora of New South Wales*, 8 vols. Government Printer, Sydney.

Published in 77 parts. Taxa treated in no particular order. Each species described in detail, with copious notes on ecology, economic botany etc. Most illustrated with lithographs and/or photographs.

Rodway, L. (1903), *The Tasmanian Flora*. Government Printer, Hobart.

A very concise Flora with many line drawings, covering 1286 species (including aliens); based on the Bentham & Hooker system.

Diels, L. & Pritzel, E. (1904–1905), Fragmenta Phytographiae Australiae Occidentalis, *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 35, 1: 55–662.

The results of extensive work in southern Western Australia; includes the description of many new species.

Dixon, W.A. (1906), *The Plants of New South Wales*. Angus & Robertson, Sydney.

Keys to families, genera and species of flowering plants and ferns, arranged in the Bentham & Hooker system.

Black, J.M. (1909), *The Naturalised Flora of South Australia*. Privately published, Adelaide.

The first floristic work on introduced plants written in Australia, concisely covering 368 species; many line drawings. Arranged in the Bentham & Hooker system.

Ewart, A.J. [assisted by Tovey, J.R.] (1909), *The Weeds, Poison Plants, and Naturalised Aliens of Victoria*. Government Printer, Melbourne.

Part I: a description and discussion of the more important poison plants and weeds; illustrated.

Part II: a census of 364 naturalised aliens and introduced exotics, with general distribution, country of origin and date of first record. Arranged in alphabetical order, but with a supplementary list of families arranged according to the Bentham & Hooker system.

Bailey, F.M. (1909)[1913], *Comprehensive Catalogue of Queensland Plants, both Indigenous and Naturalised*. Government Printer, Brisbane.

A census with authorities and, for some species, supplementary notes; line and colour illustrations. Arranged in the Bentham & Hooker system.

Domin, K. (1913–1915), *Beiträge zur Flora und Planzengeographie Australiens. Teil 1, Abt. 1 Pteridophyta & Abt. 2 Gymnospermae, Monocotyledonae*. Schweizerbart, Stuttgart. *Bibliotheca Botanica* Band 20, Heft 85.

A partial Flora based mainly on Domin's and Amalie Dietrich's collections from eastern Queensland and those of Capt A.A.Dorrien Smith (south-western Western Australia) and of Dr E.Clements (north-western Western Australia), and other collections in Kew. The final part (Dicotyledonae) appeared in 1921–1930.

Rodway, L. (1914–1916), *Tasmanian Bryophyta, Vol. I, Mosses; Vol. II, Hepatics*. The Royal Society of Tasmania, Hobart.

First published as a series of papers in *Pap. & Proc. Roy. Soc. Tasmania* (1912–1916). Synopses of families and higher taxa; keys to species in genera with more than one species.

Maiden, J.H. & Betche, E. (1916), *A Census of New South Wales Plants*. Government Printer, Sydney.

A systematic census, with bibliography of the original publication of each species and a reference to the description in *Flora Australiensis*. Arranged in the Engler system.

Ewart, A.J. & Davies, O.B. (1917), *The Flora of the Northern Territory*. McCarron & Bird, Melbourne.

The only complete Flora yet issued for the Northern Territory. Adapted from *Flora Australiensis*, with the addition of species described subsequently, together with illustrations and new locality records. Basically an expanded key, with descriptions only of the additional taxa; also includes a tabular key to families.

Domin, K. (1921–1930), *Beiträge zur Flora und Planzengeographie Australiens. Abt. 3 Dicotyledonae*. Schweizerbart, Stuttgart. *Bibliotheca Botanica* Band 22, Heft 89.

Final part of Domin (1913–1915).

Black, J.M. (1922–1929), *Flora of South Australia*, Parts I–IV; 2nd edn, Parts I–III, 1943–1952, Part IV revised by E.L.Robertson, 1957, *Supplement* by H.Eichler, 1965; Part 1, 3rd edn, edited by J.P.Jessop, 1978. Government Printer, Adelaide.

A concise, original Flora with many illustrations, arranged in the Engler system. Superseded by Jessop & Toelken (1986).

Francis, W.D. (1929), *Australian Rain-Forest Trees Excluding the Species Confined to the Tropics*. Government Printer, Brisbane.

Detailed descriptions of families, genera and species, with photographs of all species. A second edition was produced in 1951 and a third in 1970. Superseded by Floyd (1989).

Ewart, A.J. (1930)[1931], *Flora of Victoria*. Government Printer, Melbourne.

A concise, original Flora with many line drawings; describes about 2200 indigenous species and 500 naturalised species. Arranged in the Engler System.

Gardner, C.A. (1930–1931), *Enumeratio Plantarum Australiae Occidentalis: a Systematic Census of the Plants Occurring in Western Australia*. Government Printer, Perth.

The first census of the flora of Western Australia, arranged in the Engler system.

Cleland, J.B. (1934–1935), *Toadstools and Mushrooms and Other Larger Fungi of South Australia*. Government Printer, Adelaide.

Keys to families, genera and species, with concise descriptions and many illustrations. Covers Basidiomycetes, Gasteromycetes, Heterobasidiae and Myxomycetes. Classification modified from C.Rea (1922) and P.Clausen, *in* Engler & Prantl (1928), with some groups based on the work of other authors. Superseded by Grgurinovic (1997).

Lucas, A.H.S. (1936–1947), *The Seaweeds of South Australia, Part I, Introduction and the Green and Brown Seaweeds; Part II, The Red Seaweeds* (completed by F.Perrin, H.B.S.Womersley & J.R.Harris). Government Printer, Adelaide.

Keys, descriptions and black-and-white illustrations; arranged in the system of De Toni.

1951–1970

Gardner, C.A. (1952), *Flora of Western Australia*, Vol. 1, part 1, *Gramineae*. Government Printer, Perth.

The only part published of a proposed State Flora.

Blackall, W.E. & Grieve, B.J. (1954–1980), *How to Know Western Australian Wildflowers*, Parts I–IV, IIIA; Parts I–III reprinted in one volume, 1974. University of Western Australia Press, Perth.

Illustrated keys to the flora of southern Western Australia.

Wakefield, N.A. (1955), *Ferns of Victoria and Tasmania, with Descriptive Notes and Illustrations of the 116 Native Species*. Field Naturalists' Club of Victoria, Melbourne.

For many years, the most comprehensive account of ferns in these States. A second edition appeared in 1975.

Curtis, W.M. (1956–1994), *The Student's Flora of Tasmania*, Parts 1–3, 4A, 4B. Part 1 (2nd edn) by W.M.Curtis & D.I.Morris, 1975. Government Printer, Hobart.

A concise Flora with many line drawings. Arranged in the Bentham & Hooker system.

Hall, N., Johnston, R.D. & Hamilton, C.D. (1957), *Forest Trees of Australia*. Australian Government Publishing Service, Canberra.

Detailed descriptions, distribution maps and photographs of the major forest trees of Australia. Second and third editions by N.Hall, R.D.Johnston & G.M.Chippendale appeared in 1962 and 1970 respectively, and a fourth edition by D.J.Boland, M.I.H.Brooker, G.M.Chippendale, N.Hall, B.P.M.Hyland, R.D.Johnston, D.A.Kleinig & J.D.Turner appeared in 1984. Most editions were reprinted several times.

Specht, R.L. & Mountford, C.P. (eds) (1958), *American-Australian Scientific Expedition to Arnhem Land, 1948. Records 3: Botany and Plant Ecology*. Melbourne University Press, Melbourne.

Catalogue of the expedition collections, cryptogams as well as phanerogams, with description of a number of new taxa; chapters on phytogeography and ecology.

Flora of New South Wales (1961–1978). Government Printer, Sydney. Published as a Flora Series of *Contributions from the New South Wales National Herbarium*, and from 1971 as *Flora of New South Wales*.

An incomplete and now discontinued series, by various contributors, written on a monographic basis; based on the Engler system. Superseded by Harden (1990–1993).

Willis, J.H. (1962, 1972)[1973], *A Handbook to Plants in Victoria*, 2 vols. Melbourne University Press, Melbourne.

A very concise State Flora in the form of an amplified key.

Beadle, N.C.W., Evans, O.D. & Carolin, R.C. (1962)[1963], *Handbook of the Vascular Plants of the Sydney District and Blue Mountains*. Privately published, Armidale.

Contains keys to families, genera and species, with generic diagnoses. Includes Pteridophyta, Gymnospermae and Angiospermae. Systematic arrangement of families modified from Hutchinson (1926). Superseded by *Flora of the Sydney Region* (Beadle *et al.*, 1972).

Burbidge, N.T. (1963), *Dictionary of Australian Plant Genera: Gymnosperms and Angiosperms*. Angus & Robertson, Sydney.

For each genus includes important bibliography, general distribution and number of species.

Wetmore, C.M. (1962)[1964], Catalogue of the lichens of Tasmania, *Revue Bryologique et Lichénologique* 32: 223–264.

Checklist only. Superseded by Kantvilas (1989).

Beard, J.S. (ed.) (1965), *Descriptive Catalogue of West Australian Plants*; 2nd edn 1970, as *West Australian Plants*. Society for Growing Australian Plants, Sydney.

A census of the flowering plants of Western Australia with brief notes on the habit, habitat and distribution, based on the collections at the Western Australian Herbarium.

Stones, M. & Curtis, W.M. (1967–1978), *The Endemic Flora of Tasmania*, 6 vols. Ariel Press, London.

Paintings by Margaret Stones and text by Winifred Curtis.

Burbidge, N.T. & Gray, M. (1970), *Flora of the A.C.T. [Australian Capital Territory]* Australian National University Press, Canberra.

A concise illustrated Flora of the Australian Capital Territory set out as amplified keys, arranged in the Engler system.

1971–1980

Beadle, N.C.W. (1971–1987), *Student's Flora of North Eastern New South Wales*, Parts I–VI. University of New England, Armidale.

A concise systematic Flora in the form of amplified keys, together with generic descriptions. Arranged in a modified Hutchinson system.

Beadle, N.C.W., Evans, O.D. & Carolin, R.C. (1972), *Flora of the Sydney Region*. A.H. & A.W.Reed, Sydney.

Revised, enlarged and illustrated edition of Beadle *et al.*, (1962). A third edition was published in 1982; a fourth edition in 1994.

Chippendale, G.M. (1972), Check list of Northern Territory plants, *Proceedings of the Linnean Society of New South Wales* 96: 207–267.

A census with abbreviated distributions, arranged in the Engler system.

Weber, W.A. & Wetmore, C.M. (1972), Catalogue of the Lichens of Australia, exclusive of Tasmania, *Beihefte zur Nova Hedwigia* 41: 1–137.

An alphabetical list with references, synonyms and distributions by States.

Everist, S.L. (1974), *Poisonous Plants of Australia*. Angus & Robertson, Sydney.

Scientific and common names, brief descriptions, symptoms, treatments. A second edition of this classic work appeared in 1981.

Scott, G.A.M., Stone, I. & Rosser, C. (1976), *The Mosses of Southern Australia*. Academic Press, London.

The mosses of the region described or diagnosed, together with keys and many illustrations.

Jones, D.L. & Clemesha, S.C. (1976), *Australian Ferns and Fern Allies with Notes on their Cultivation*. A.H. & A.W.Reed, Sydney.

Descriptions, distributions, line drawings. A second edition appeared in 1981.

Aston, H.I. (1977), *Aquatic Plants of Australia*. Melbourne University Press, Melbourne.

Arranged alphabetically by family in major groups (ferns, dicotyledons, monocotyledons) with detailed descriptions, keys to species, notes on ecology and distribution, copious line drawings.

Burbidge, N.T. (1978), *Plant Taxonomic Literature in Australian Libraries*. CSIRO/ABRS, Canberra.

Availability of Australian and overseas plant taxonomic works in 49 public and institutional libraries. Includes bibliographic details.

Costin, A.B., Gray, M., Totterdell, C. & Winbush, D. (1979), *Kosciusko Alpine Flora*. CSIRO & William Collins, Melbourne.

Keys and descriptions for the vascular flora, together with descriptions of the plant communities and history of the region. Copiously illustrated in colour. Arranged according to the Engler system.

Filson, R.B. & Rogers, R.W. (1979), *Lichens of South Australia*. Government Printer, Adelaide.

Keys and diagnoses to species level.

Catcheside, D.G. (1980), *Mosses of South Australia*. Government Printer, Adelaide.

Keys and descriptions, with line and colour illustrations. Arranged according to the system of M.Fleischer.

Clifford, H.T. & Constantine, J. (1980), *Ferns, Fern Allies and Conifers of Australia. A Laboratory Manual*. University of Queensland Press, Brisbane.

Generic level descriptions, keys to species.

Elliot, W.R. & Jones, D.L. (1980–), *Encyclopaedia of Australian Plants Suitable for Cultivation*. Lothian, Melbourne.

A multivolume work, arranged alphabetically by genus and species. Each species briefly described, with notes on cultivation requirements. Line drawings and coloured photographs. Supplements are being published (1994–).

1981–1990

Leigh, J., Briggs, J. & Hartley, W. (1981), *Rare or Threatened Australian Plants*. Special Publication No. 7, Australian National Parks and Wildlife Service, Canberra.

Checklist; families in systematic order, genera and species alphabetic; risk code; distribution by State and Region. Superseded by Briggs & Leigh (1995).

Green, J.W. (1981), *Census of the Vascular Plants of Western Australia*. Western Australian Herbarium, South Perth.

A list of the native and naturalised flora of the State, with families arranged in the Engler system. A second edition appeared in 1985, with synonyms and floristic tables.

Jessop, J.P. (ed.) (1981), *Flora of Central Australia*. A.H. & A.W.Reed, Sydney.

A multi-author concise Flora of the arid regions of Australia, arranged in the Engler system.

Cunningham, G.M., Mulham, W.E., Milthorpe, P.L. & Leigh, J.H. (1981), *Plants of Western New South Wales*. Soil Conservation Service of New South Wales & Government Printer, Sydney.

Describes over 2000 species, mostly illustrated in colour or black-and-white, with keys to some groups. Families arranged in the Engler system; genera and species arranged alphabetically.

Flora of Australia (1981–). Vol. 1, Introduction (1981; 2nd edn, 1998); Vol. 3, Hamamelidales to Casuarinales (1989); Vol. 4, Phytolaccaceae to Chenopodiaceae (1984); Vol. 8, Lecythidales to Batales (1982); Vol. 12, Mimosaceae (excl. Acacia), Caesalpiniaceae (1998); Vol. 16, Elaeagnaceae, Proteaceae 1 (1995); Vol. 18, Podostemaceae to Combretaceae (1990); Vol. 19, Myrtaceae — *Eucalyptus, Angophora* (1988); Vol. 22, Rhizophorales to Celastrales (1984); Vol. 25, Melianthaceae to Simaroubaceae (1985); Vol. 28, Gentianales (1996); Vol. 29, Solanaceae (1982); Vol. 35, Brunoniaceae, Goodeniaceae (1992); Vol. 45, Hydatellaceae to Liliaceae (1987); Vol. 46, Iridaceae to Dioscoreaceae (1986); Vol. 48, Ferns, Gymnosperms and Allied Groups (1998); Vol. 49, Oceanic Islands 1 (1994); Vol. 50, Oceanic Islands 2 (1993); Vol. 54, Lichens – Introduction, Lecanorales 1 (1992); Vol. 55, Lichens – Lecanorales 2, Parmeliaceae (1994). Published by Australian Government Publishing Service until 1994 (Vol. 49), then by ABRS/CSIRO Australia (Vol. 55 onwards).

Rogers, R.W. (1981), *The Genera of Australian Lichens (Lichenized Fungi)*. University of Queensland Press, St Lucia.

Keys to the accepted genera of Australian lichens, with descriptions and notes on chemistry, phycobionts and distribution of each.

Sainty, G.R. & Jacobs, S.W.L. (1981), *Waterplants of New South Wales*. Water Resources Commission of New South Wales, Sydney.

Taxa arranged alphabetically by family, genus and species within major groups. Descriptions, notes on biology, copious coloured photographs.

Morley, B.D. & Toelken, H.R. (eds) (1983), *Flowering Plants in Australia*. Rigby Publishers, Adelaide.

A multi-author work providing synopsies of Australian vascular plant families, with keys to genera, notes on species numbers, maps of family distribution, and line and colour illustrations. Arranged according to the Takhtajan scheme.

Stanley, T.D. & Ross, E.M. (eds) (1983–1989), *Flora of South-Eastern Queensland*. Queensland Department of Primary Industries, Brisbane.

A concise Flora of the Moreton, Wide Bay, Burnett and Darling Downs Pastoral Districts of south-eastern Queensland, covering about 3600 species of flowering plants. Based on an Englerian system of classification; contains keys, descriptions and notes on distribution and ecology; many species illustrated.

Filson, R.B. (1983), *Checklist of Australian Lichens*. National Herbarium of Victoria, Melbourne.

List of all names reported as having been applied to Australian species. Arranged alphabetically by genus and species; limited synonymy; distribution by State. A second edition by the same author and publisher appeared in 1986, and a third edition in 1988. The list was restructured and updated by McCarthy (1991), and again by Filson (1996).

Leigh, J., Boden, R. & Briggs, J. (1984), *Extinct and Endangered Plants of Australia*. Macmillan, South Melbourne.

Descriptions, maps and illustrations of 76 presumed extinct and 203 endangered species from Australia, with brief notes on ecology, reservation status, and cultivation status.

Womersley, H.B.S. (1984), *The Marine Benthic Flora of Southern Australia. Part 1. Introduction; Collection and Preservation; History of Studies; Ecology; Biogeography; Seagrasses; Chlorophyta and Charophyta*. Flora and Fauna Handbooks Committee, Adelaide.

A comprehensive Flora of marine algae of the southern Australian shoreline, from about Kalbarri in Western Australia to eastern Victoria, with keys, detailed descriptions from Phylum to infraspecific level, distribution, synonymy, typification and lists of specimens examined; copiously illustrated. Other groups are dealt with in Womersley (1987, 1994, 1996).

Scott, G.A.M. (1985), *Southern Australian Liverworts*. Australian Flora & Fauna Series No. 2. Australian Government Publishing Service, Canberra.

Keys, brief descriptions of genera and species, and distribution of the liverworts of Victoria and adjacent areas, copiously illustrated with line drawings and halftone illustrations.

Filson, R.B. (1986), *Index to Type Specimens of Australian Lichens: 1800–1984*. Australian Flora & Fauna Series No. 4. Australian Government Publishing Service, Canberra.

A list of all lichen names based on Australian collections, with Type details for each.

Dunlop, C.R. & Bowman, D.M.J.S. (1986), *Atlas of the Vascular Plant Genera of the Northern Territory*. Australian Flora & Fauna Series No. 6. Australian Government Publishing Service, Canberra.

Maps of the distribution of vascular plants in the Northern Territory, at generic level.

Jessop, J.P. & Toelken, H.R. (1986), *Flora of South Australia*, 4 vols. Flora and Fauna of South Australia Handbooks Committee, Adelaide.

Successor to Black's *Flora* (1922–1978), keying and describing over 3600 vascular plant species. For each species there are notes on distribution and ecology, and a full South Australian synonymy; illustrated.

Duncan, B.D. & Isaac, G. (1986), *Ferns and Allied Plants of Victoria, Tasmania and South Australia with Distribution Maps for the Victorian Species*. Melbourne University Press, Carlton.

Descriptions, keys, maps of Victorian distribution, line drawings, coloured and half-tone photographs.

Filson, R.B. (1987), *A Census of the Non-vascular Plants of Victoria. 1: Lichens*. National Herbarium of Victoria, Melbourne.

Records taken from Australian list of 1986 (see above under Filson (1983)).

Womersley, H.B.S. (1987), *The Marine Benthic Flora of Southern Australia. Part 2. Phaeophyta and Chrysophyta* (Vaucheria). Flora and Fauna Handbooks Committee, Adelaide.

A continuation of Womersley (1984).

Marchant, N.G., Wheeler, J.R., Rye, B.L., Bennett, E.M., Lander, N.S. & Macfarlane, T.D. (1987), *Flora of the Perth Region*. Western Australian Herbarium, Perth.

A well-illustrated concise Flora covering 10 500 sq. km of the coastal plain, Darling Scarp and the western part of the Darling Range, centred on Perth. Contains keys, descriptions and notes on ecology and distribution. The classification is approximately that of Cronquist for the dicotyledons and Dahlgren & Clifford for the monocotyledons.

Kantvilas, G. & James, P.W. (1987), The macrolichens of Tasmanian rainforest: key and notes, *Lichenologist* 19: 1–28.

Taxonomic notes and dichotomous key. Reissued in revised form by Kantvilas (1995).

Dyne, G.R. & Walton, D.W. (eds) (1987), *Fauna of Australia. Vol. 1A, General Articles*. Australian Government Publishing Service, Canberra.

Contains a number of very useful review articles on Australian geological history, climate, marine, terrestrial and freshwater environments, history of scientific discovery, and faunal evolution and radiation.

Streimann, H. & Curnow, J. (1989), *Catalogue of Mosses of Australia and its External Territories*. Australian Flora & Fauna Series No. 10. Australian Government Publishing Service, Canberra.

A list of all names used in the Australian moss flora, with places of publication, indications of synonymy, lists of secondary literature, and distribution.

Buchanan, A.M., McGeary-Brown, A. & Orchard, A.E. (1989), *A Census of the Vascular Plants of Tasmania*. Tasmanian Herbarium Occasional Publication Number 2, Hobart.

Checklist of all vascular plants of Tasmania.

Kantvilas, G. (1989), A checklist of Tasmanian lichens, *Papers and Proceedings of the Royal Society of Tasmania* 117: 41–51.

An annotated list of accepted names. An updated list by the same author appeared in *Muelleria* 8: 155–175 (1994).

Sammy, N. (1989), Checklist of Western Australian lichens, *Mycotaxon* 35: 417–428.

History of studies and checklist of taxa recorded in Western Australia.

Floyd, A.G. (1989), *Rainforest Trees of Mainland South-eastern Australia*. Inkata Press, Melbourne & Sydney.

A successor to Francis (1929, 1951, 1970). Detailed descriptions of 385 species from Victoria and New South Wales; keys, line drawings of all species.

Andrews, S.B. (1990), *Ferns of Queensland. A Handbook to the Ferns and Fern Allies*. Queensland Department of Primary Industries, Brisbane.

A Flora account of these groups, with keys and full descriptions; illustrated with line drawings.

Hnatiuk, R.J. (1990), *Census of Australian Vascular Plants*. Australian Flora & Fauna Series No. 11. Australian Government Publishing Service, Canberra.

Brings together data from the State Herbaria on species and distribution, under a unified nomenclature. Covers 15 638 native and 1952 naturalised species, and over 1300 infraspecific taxa, in 103 distributional categories. Now amalgamated with the *Australian Plant Name Index* (Chapman, 1991), and available electronically through the World Wide Web.

Harden, G.J. (1990–1993), *Flora of New South Wales*, 4 vols. New South Wales University Press, Kensington.

A concise Flora, with keys and descriptions, and brief notes on distribution and ecology. Copiously illustrated, with each species having at least one line drawing; many colour plates.

1991–present

Chapman, A.D. (1991), *Australian Plant Name Index*. Australian Flora & Fauna Series Nos 12–15. Australian Government Publishing Service, Canberra.

A catalogue of all scientific names used for vascular plants in Australia, with details of place of publication, typification, location of Type specimens, references to modern literature and notes on nomenclature. Over 62 000 names are listed. Now amalgamated with *Census of Australian Vascular Plants* (Hnatiuk, 1990), and available electronically through the World Wide Web.

McCarthy, P.M. (1991), *Checklist of Australian Lichens, Fourth Edition*. National Herbarium of Victoria, Melbourne.

A restructured and updated version of Filson (1983, 1986, 1988).

Dalton, P.J., Seppelt, R.D. & Buchanan, A.M. (1991), An annotated checklist of Tasmanian mosses, *in* M.R.Banks, S.J.Smith, A.E.Orchard & G.Kantvilas (eds), *Aspects of Tasmanian Botany. A Tribute to Winifred Curtis*, pp. 15–32. Royal Society of Tasmania, Hobart.

Checklist with synonymy, arranged alphabetically by family, genus and species.

Wheeler, J.R. (ed.), Rye, B.L., Koch, B.L. & Wilson, A.J.G. (1992), *Flora of the Kimberley Region*. Western Australian Herbarium, Como.

A well-illustrated concise Flora covering 2085 species from the Kimberley Region, an area of about 300 000 sq. km comprising the Northern Botanical Province of Western Australia. The content, arrangement and style follow that of the *Flora of the Perth Region* (Marchant *et al.*, 1987).

McCarthy, P.M. (1992), *Bibliography of Australian Lichens: 1807–1991*. National Herbarium of Victoria, Melbourne.

A compilation from books and 145 journals of all papers dealing with Australian lichens, with a note on the subject and geographical coverage of each.

Jessop, J.P. (ed.) (1993), *A List of the Vascular Plants of South Australia (Edition IV)*. Botanic Gardens of Adelaide & State Herbarium, Adelaide.

A checklist of 4527 names, with families in a basically Englerian sequence; genera and species alphabetical.

Henderson, R.J.F. (ed.) (1993), *Queensland Vascular Plants. Names and Distribution*. Queensland Herbarium, Indooroopilly.

An alphabetical listing of 8504 species, with coded indications of distribution within Queensland, and elsewhere. Superseded by Henderson (1997).

Foreman, D.B. & Walsh, N.G. (eds) (1993), *Flora of Victoria. Volume 1, Introduction*. Inkata Press, Melbourne & Sydney.

Introductory essays on history, geology, climate, soils, vegetation etc., for a 4-volume Flora of the State, to replace that of Willis (1962, 1972). For taxonomic treatments, see Walsh & Entwisle (1994, 1996).

Hyland, B.P.M. & Whiffin, T. (1993), *Australian Tropical Rain Forest Trees. An Interactive Identification System*. CSIRO Publishing, East Melbourne.

A multimedia package consisting of an interactive computer key (MS-DOS or Macintosh) plus two printed manuals, allowing the identification of over 1000 species of Australian rainforest trees. The manuals provide an illustrated glossary, and for each species give descriptions, distribution and ecology, and scientific, common and trade names.

Christophel, D.C. & Hyland, B.P.M. (1993), *Leaf Atlas of Australian Tropical Rain Forest Trees*. CSIRO Publishing, East Melbourne.

A supplement to Hyland & Whiffin (1993), providing approximately life-sized low voltage x-ray photographs of leaves of over 1000 species.

Lazarides, M. & Hince, B. (eds) (1993), *CSIRO Handbook of Economic Plants of Australia* (revised edn). CSIRO Publishing, East Melbourne.

An alphabetical listing by scientific name of the native, naturalised and cultivated vascular plants of economic importance in Australia, with maps of distribution by State or Territory, and comprehensive lists of common names. This book is an expanded and revised version of two earlier publications, *Standardized Plant Names* (Anon., CSIRO, 1942, 1953) and *A Checklist of Economic Plants in Australia* (W.Hartley, 1979).

Womersley, H.B.S. (1994), *The Marine Benthic Flora of Southern Australia. Rhodophyta. Part IIIA, Bangiophyceae and Florideophyceae (Acrochaetiales, Nemaliales, Gelidiales, Hildenbrandiales and Gigartinales* sensu lato*)*. Flora of Australia Supplementary Series Number 1. ABRS, Canberra.

A continuation of Womersley (1984, 1987).

Ramsay, H.P. & Seur, J. (1994), *Register of Type Specimens of Mosses in Australian Herbaria*. Flora of Australia Supplementary Series Number 2. ABRS, Canberra.

A catalogue of all moss Type specimens located in Australian herbaria, with details of the place of publication of each name, protologue citation, and details of Type and putative Type specimens, including place of lodgement.

Liddle, D.T., Russell-Smith, J., Brock, J., Leach, G.J. & Connors, G.T. (1994), *Atlas of the Vascular Rainforest Plants of the Northern Territory*. Flora of Australia Supplementary Series Number 3. ABRS, Canberra.

Distribution maps for each of 604 vascular rainforest species, based on 58 783 survey records and 21 187 herbarium specimens, with notes on biogeography and conservation status.

Walsh, N.G. & Entwisle, T.J. (eds) (1994), *Flora of Victoria Volume 2, Ferns and Allied Plants, Conifers and Monocotyledons*. Inkata Press, Melbourne & Sydney.

Second of a multi-author 4-volume Flora, with keys, descriptions, synonymy, distribution and ecology of Victoria's vascular flora. Distribution map for each species; richly illustrated with both black-and-white line drawings and colour paintings. See also Foreman & Walsh (1993) and Walsh & Entwisle (1996).

Day, S.A., Wickham, R.P., Entwisle, T.J. & Tyler, P.A. (1995), *Bibliographic Checklist of Non-marine Algae in Australia*. Flora of Australia Supplementary Series Number 4. ABRS, Canberra.

A catalogue of all names of non-marine algae reported from Australia, with indications of synonymy, distribution and lists of secondary literature.

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First part of a proposed 4-volume, well-illustrated concise Flora, covering Bathurst and Melville Islands, and the mainland area bounded by the Daly River, the town of Pine Creek and the western border of Kakadu National Park. The 440 species (Mimosaceae to Euphorbiaceae) are keyed and described, and notes on ecology and distribution are provided.

Dunlop, C.R., Leach, G.J., Latz, P.K., Barritt, M.J., Cowie, I.D. & Albrecht, D.E. (1995), *Checklist of the Vascular Plants of the Northern Territory, Australia. Family Ordered*. Conservation Commission of the Northern Territory, Darwin.

An alphabetical listing of 3969 species (4179 taxa), with coded notes on conservation status and distribution.

Kantvilas, G. (1995), A revised key and checklist for the macrolichens in Tasmanian cool temperate rainforest, *Tasforests* 7: 93–127.

Update of Kantvilas & James (1987).

Spencer, R.D. (1995), *Horticultural Flora of South-eastern Australia: The Identification of Garden and Cultivated Plants. Vol. 1, Ferns, Conifers & Their Allies*. University of New South Wales Press, Sydney.

Descriptions, keys, illustrations, bibliography, glossary. Covers both native and exotic species. First of 4 volumes planned.

Briggs, J.D. & Leigh, J.H. [1996](1995), *Rare or Threatened Australian Plants*, rev. edn. CSIRO, Collingwood.

Alphabetical listing of the rare or threatened vascular flora, with rarity codes and reservation status for each. Supersedes Leigh, Briggs & Hartley (1981).

Womersley, H.B.S., Woelkerling, W.J., Harvey, A.S., Penrose, D.L. & Johansen, H.W. (1996), *The Marine Benthic Flora of Southern Australia. Rhodophyta. Part IIIB, Gracilariales, Rhodymeniales, Corallinales and Bonnemaisoniales*. Flora of Australia Supplementary Series Number 5. ABRS, Canberra.

A continuation of Womersley (1984, 1987, 1994).

Filson, R.B. (1996), *Checklist of Australian Lichens and Allied Fungi*. Flora of Australia Supplementary Series Number 7. ABRS, Canberra.

An update, expansion and restructuring of the earlier lists of Filson (1983, 1986, 1988) and of McCarthy (1991).

Walsh, N.G. & Entwisle, T.J. (eds) (1996), *Flora of Victoria Volume 3, Dicotyledons: Winteraceae to Myrtaceae*. Inkata Press, Melbourne & Sydney.

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Garrett, M. (1996), *The Ferns of Tasmania. Their Ecology and Distribution*. Tasmanian Forest Research Council, Hobart.

Distribution (including map), ecology and excellent colour photographs of the ferns and fern allies of Tasmania.

Fungi of Australia (1996–), Vol. 1A, Introduction–Classification (1996); Vol. 1B, Introduction–Fungi in the Environment (1996); Vol. 2A, Catalogue and Bibliography of Australian Macrofungi 1. Basidiomycota *p.p.* (1997). ABRS/CSIRO Australia.

First of a proposed 60-volume series which will provide Flora-type accounts of the fungi (*sens. lat.*) of Australia. The first three volumes (above) provide introductory essays, keys to Orders, glossary and a classification framework (Vols 1A and 1B), and the first part of a census, bibliography and synonymy of Australian macrofungi (Vol. 2A).

Grgurinovic, C. (1997), *Larger Fungi of South Australia*. Botanic Gardens of Adelaide & State Herbarium/Flora & Fauna Handbooks of South Australia Committee, Adelaide.

Successor to Cleland (1934–1935).

Henderson, R.J.F. (ed.) (1997), *Queensland Plants. Names and Distribution*. Queensland Herbarium, Brisbane.

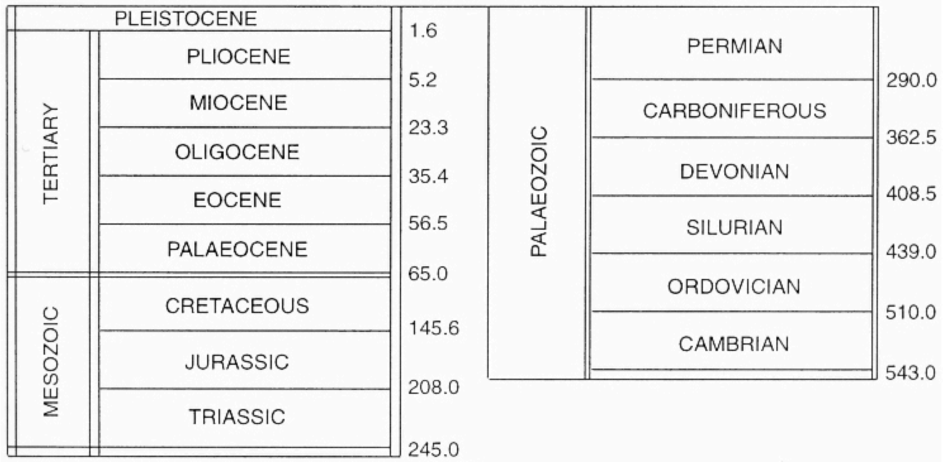
Successor to Henderson (1993), updated and expanded to cover, in addition, algae, lichens and mosses.

EVOLUTION OF AUSTRALIAN ENVIRONMENTS

L.A.Frakes[1]

Australian environments of the past have been influenced by the geological evolution of the continent as a result of its changing position on the globe, the evolution of its landforms, and wide swings in the global climate. The Australian vegetation has, in its turn, been affected by these changes, and perhaps equally as profoundly by the nature of the ancestral vegetation before the continent separated from Gondwana, by the ways in which the endemic floras evolved, and by occasional immigrants. Here the controls on palaeoenvironments exerted by the evolution of the continent itself over Phanerozoic time, that is, roughly the last 540 million years, are addressed. The foundation for discussion of continental movements and attendant palaeogeographic connections to other landmasses is provided by the work of Veevers (1984, 1991a), which also elucidates some of the developments in landform transformations. Detailed examinations of the most recent landforms and of the climatic history are based on a range of important publications, notably Langford *et al.* (1995) and Hill (1994). Study of the deduced trends in these variables and their interactions can lead to an integrated picture of how a changing Australia contributed to a history of changing vegetation.

In any geological history it is imperative to specify the time scale used. There are many such scales, both those relating to a part of Phanerozoic time and others which cover the whole of this enormous span of time. Scales differ mainly in the numerical ages assigned to boundaries between named Periods, Epochs or Ages, three representations of geologic time corresponding to progressively shorter spans of time. In this study, I employ a slightly modified version of the Phanerozoic time scale of Harland *et al.* (1990) (Fig. 31), a recently published and comprehensive effort. The appropriate sedimentary basins of Australia, important because they contain the record of palaeo-environments over geological time, are shown in Fig. 32.



	PLEISTOCENE	1.6
TERTIARY	PLIOCENE	5.2
	MIOCENE	23.3
	OLIGOCENE	35.4
	EOCENE	56.5
	PALAEOCENE	65.0
MESOZOIC	CRETACEOUS	145.6
	JURASSIC	208.0
	TRIASSIC	245.0
PALAEOZOIC	PERMIAN	290.0
	CARBONIFEROUS	362.5
	DEVONIAN	408.5
	SILURIAN	439.0
	ORDOVICIAN	510.0
	CAMBRIAN	543.0

Figure 31. Geological Time Scale used in this chapter. Ages in millions of years (Ma) Modified from Harland *et al.*, 1990.

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Australian palaeogeography

In considering the history of Australian vegetation, palaeogeography plays an important role. Location of the continent on the globe, particularly its latitudinal range and its spatial relationships to neighbouring seas, contributes strongly to the types and range of climates experienced by the continent, environmental factors of major significance for floras. Connections with adjacent or nearby landmasses determine the extent of migrations of exotic taxa, at least by land. Other aspects of palaeogeography – the topographic relief resulting from spasmodic tectonic activity and the configuration of seaways on the landmass – also influence the development and distribution of vegetation through time, by directing or restricting the dispersal of plant life. It is not intended here to present a detailed account of continental evolution but rather to provide a framework for consideration of the obvious changes in the Australian environments through time.

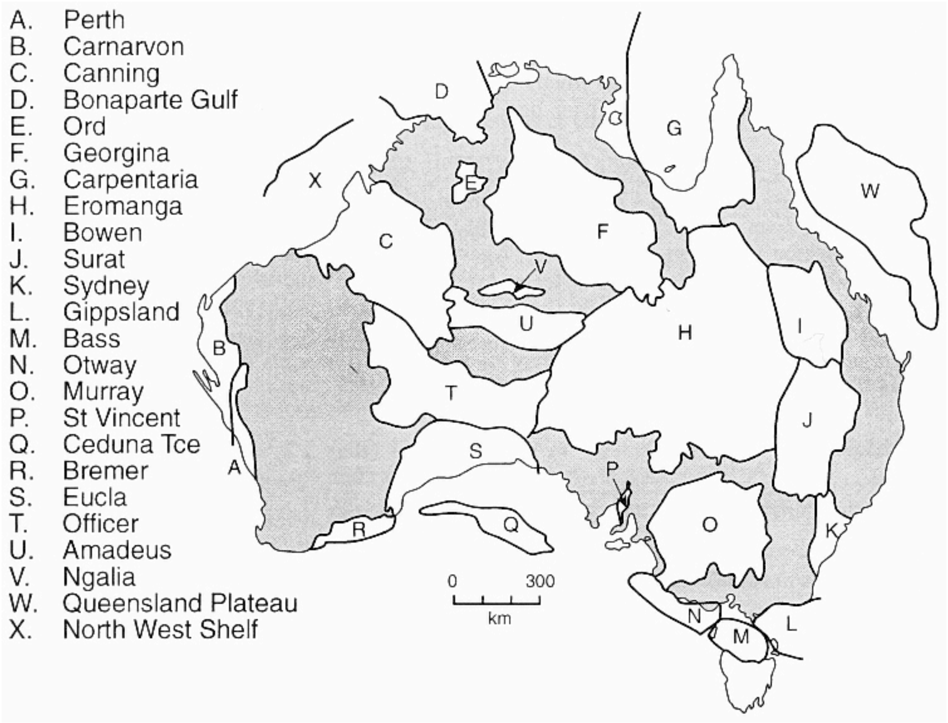

Figure 32. Phanerozoic sedimentary basins and other geological features of Australia.

Palaeolatitudes

The position of Australia on the globe has varied with motion of the continent through time (Fig. 33). The Phanerozoic saw the continent move from relatively low latitudes initially to very high latitudes in the Late Palaeozoic (Carboniferous to Permian, 363–245 million years ago (Ma)), then to mid-latitudes in the Early Mesozoic (Triassic to Jurassic, 245–145 Ma). In the early part of the Cretaceous Period (140–c. 95 Ma), the Australian landmass again occupied high latitudes, but thereafter it migrated, at first slowly but then more rapidly, to its present position in the low to mid-latitudes (Fig. 33; data from Embleton; in Veevers, 1984). This motion across lines of latitude is deduced from the inclination of the remnant magnetic field preserved in dated rocks, which is documented as a measure of latitude. The method thus determines the latitude and the orientation of latitude lines at the site from which the rock sample came; this permits the drawing of latitude lines on maps of the continent (Fig. 34). The data, however, convey no information relating to longitude of the sampling site, nor as to whether it was the magnetic/geographic pole, or the continent itself, which moved. Only relative motion between continent and pole can be specified.

Measurement errors for individual sets of samples can range from <5° for young samples to >15° of arc for older ones, and these values reflect the accuracy of the calculated latitudes. In the case of Australian positioning for the more recent past, the last 120 million years, the results from rock magnetism are supported by data from seafloor magnetic stripes in the Southern Ocean, which document the progressive northward movement of the continent. For more recent times, the location of Australia on the globe can be determined by reference to the seafloor magnetic anomalies to the south of the continent (Scotese *et al.*, 1988).

The south of Australia has not always been in the south (Fig. 33), because the direction of relative continental movement has often been oblique to both latitude and longitude. This was particularly true for intervals in earlier Phanerozoic time, when first the east and then the west instead occupied the southernmost position. Most of Australia resided in the Northern Hemisphere for much of the first 150 million years of the Phanerozoic; since about 390 Ma, the continent has been located in the Sorthern Hemisphere, twice moving to high latitudes. From its high latitude position about 110 Ma, the continent has travelled progressively northward, at first slowly but then at the present rate. The effects of these motions on climate will be discussed later, but for now it should be remembered that shifts through latitude zones presented both opportunities and limitations for the preservation and the dispersal of past floras.

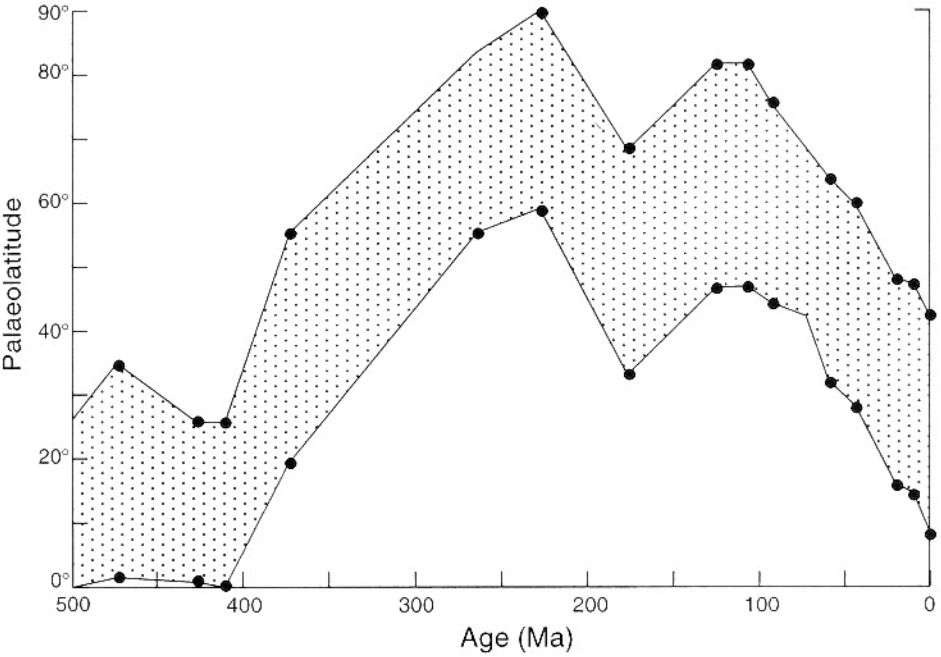

Figure 33. The latitudinal track of Australia through Phanerozoic time. Note that during rotation of the continent, various parts assume the most poleward and equatorial positions at various times. (Based on the summary of Embleton, 1984).

Relations with other landmasses

Amalgamations and drift

Australia has not travelled alone through its history. Just before the beginning of Phanerozoic time, the continent came together with all the major landmasses to form a supercontinent roughly centred on the equator and extending to the south pole. The Australian segment was located in the low to middle northern latitudes and maintained approximately the same position until the beginning of the Phanerozoic. The neighbouring continental masses consisted of Antarctica off the present southern margin, New Zealand to the east, and the Indian subcontinent and other parts of present Asia off the western margin. It has been suggested that North America lay in the region beyond and to the north of New Zealand (Fig. 35) (Moores, 1991; Dalziel, 1991). At some time in the Early Palaeozoic, the supercontinent divided into two major parts separated by the Tethys Sea – Laurasia, encompassing most of the present northern continents, and Gondwana comprising the southern continents, including Australia. Dalziel *et al.* (1994) suggest a different history: Australia as part of Gondwana was joined to North America until final separation by rifting at about 750 Ma.

The present north of our continent was situated near the border of the Tethys Sea, separated from it by part of present southern China and slivers of SE Asia. This collection of relatively small continental fragments is sometimes referred to as Cimmeria. The distance to Cimmeria may have been slight, and the gap may have been temporarily closed in the Late Devonian (Scotese *et al.*, 1985). It was not until much later, in the Jurassic and Cretaceous, that Australia left its neighbours and began to move independently.

Amalgamation of continental blocks to Australia in the Early Phanerozoic is marked by the Cambrian greenstone belts of Victoria and the deformed Early Palaeozoic rocks of eastern Australia; these can be taken to represent collision of both marine and continental fragments with what is now central Australia (Fig. 35). Later, beginning in the Devonian, accumulated blocks in the north-east included volcanic arcs related to subduction of Pacific oceanic crust (Fig. 36). This interpretation is based on evidence that much of eastern Australia, including the Lachlan Fold Belt, consists of displaced terranes exotic to the continent (Fergusson *et al.*, 1986). The distance of transport of these terranes from offshore may not have been much greater than about 100 km, judging from the age of their contained sedimentation versus the age of their deformation against the old continental margin. Overall, amalgamation and associated mountain building in this eastern sector of the continent may have ranged from Late Cambrian to Middle Devonian. Many of the data sites for Palaeozoic palaeolatitude determinations are located in the Lachlan Fold Belt, but the postulated short transport distances of these exotic blocks would suggest the measurements are valid for determining the position of the continent proper.

We now have a picture of Early Palaeozoic Australia (Fig. 36: c. 410–380 Ma), which included an adjoined large eastern block made up of much of Victoria, Tasmania, New South Wales and Queensland, as well as the possible north-western extremity consisting of part of southern China and the Himalayan fragments. The latter, now found as tectonic terranes caught up in deformed trends in Malaysia, Thailand and Burma, remained as part of Gondwanan Australia until at least the end of the Permian, judging from their faunal and lithological (e.g. Late Palaeozoic tillites) affinities.

From a palaeobiogeographical point of view, the obvious pathways for new landbased immigration in the Early Palaeozoic, that is, after the advent of landplants, were from the east and north-east via the adjoined eastern block, and possibly from the north (Cimmeria). Earlier avenues had been open from Gondwana via Antarctica and the Indian subcontinent and these continued as routes of access. However, any taxa gained through these pathways also may have originated from yet farther afield but still from within Gondwana. Because of the uncertain configuration of any join with North America, the degree of access from the Laurasian quarter is unknown. Migration routes within the continent were enhanced for marine organisms, owing to the presence of a major seaway which spanned much of the centre.

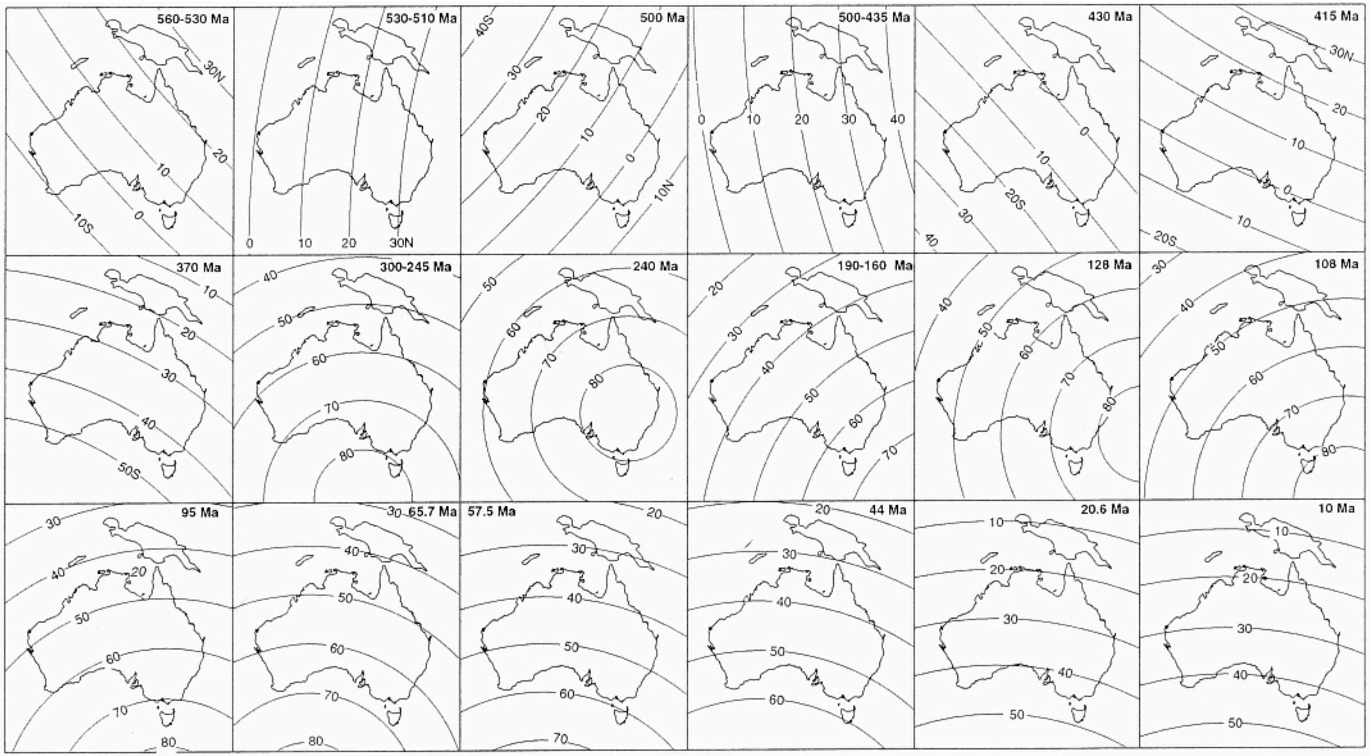

Figure 34. Palaeogeographic reconstructions showing the palaeolatitudes of Australia through the Phanerozoic (modified from Embleton, 1984).

As summarised by Veevers (1991a), the supercontinent Pangea was formed by the joining together of Gondwana and Laurasia along a suture between northern Africa and southern Europe at about 320 Ma (Carboniferous). Thus the supercontinent would have extended from pole to pole (Fig. 37). This idea radically alters the concept of Gondwana as a separate landmass on which accumulated the distinctive Gondwana sequence of sedimentary and volcanic rocks (Carboniferous to Jurassic), and the Gondwana biota. New palaeomagnetic data precisely locating the various elements are required to substantiate the temporal and geographical extent of this rejoining before judgements can be made about the efficiency or possibility of floral and faunal migrations into the Australian sector.

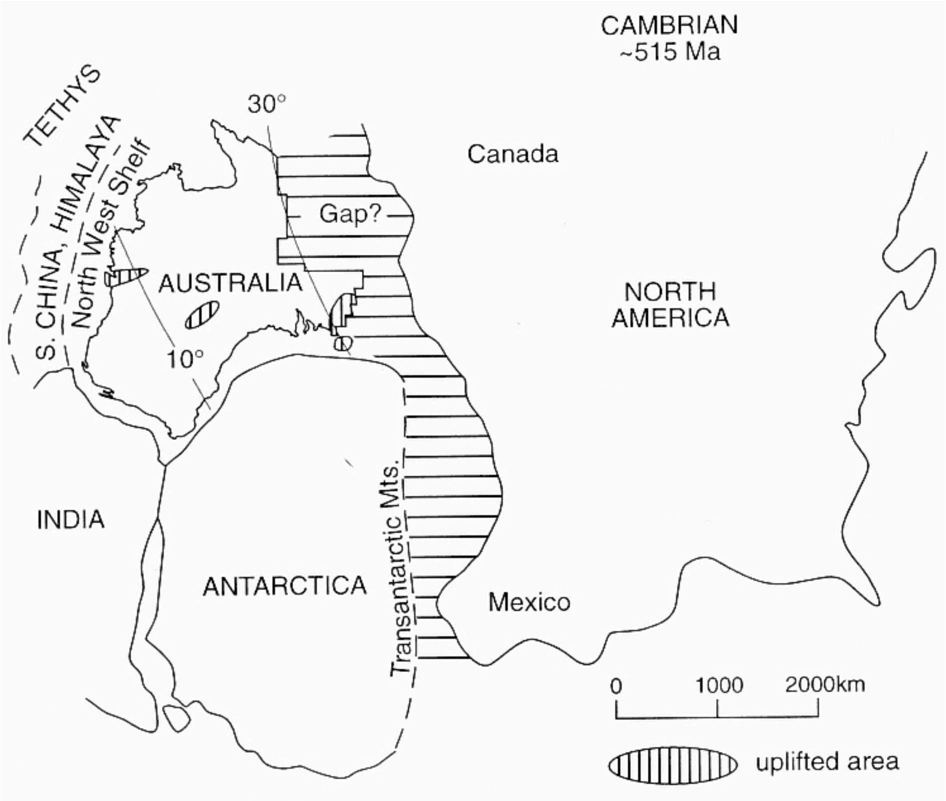

Figure 35. Palaeogeographic reconstruction of the Pacific region at about 515 Ma during the Cambrian Period. Note that there may have been a substantial gap between Australia and North America. Modified from Moores (1991). Palaeolatitudes after Embleton (1984).

Separations and drift

For our purposes, Gondwana can be considered as having existed as a continental entity during a long period, perhaps 160 million years, from about 360 Ma until sometime in the Jurassic, when a series of events began which eventually led to the isolation of Australia as a continent in its own right. The first separations took place along the northern and north-western Australian margins, with the displacement of southern China and the soon-to-be Himalayan fragments (Metcalfe, 1995). The timing of these movements is uncertain because the appropriate palaeomagnetic data is lacking. The fragments probably departed at about the same time as Gondwana began to split, with initiation of seafloor spreading in the north-eastern Indian Ocean (c. 155 Ma; Fig. 38). Within less than 10 million years, the whole of these northern terranes were separated from Australia/New Zealand/Antarctica by the northern arm of the new Indian Ocean, and all appear to have docked against various parts of Asia by about 50 Ma. Rifting, presaging spreading, created the non-marine Otway and Bight Basins along southern Australia at this time (Fig. 38). Long-established migration routes for Gondwanan floras and faunas to and from the Australian segment thus were disrupted at this time, with any direct land connections to Africa/South America severed as a consequence of the northward movement of India.

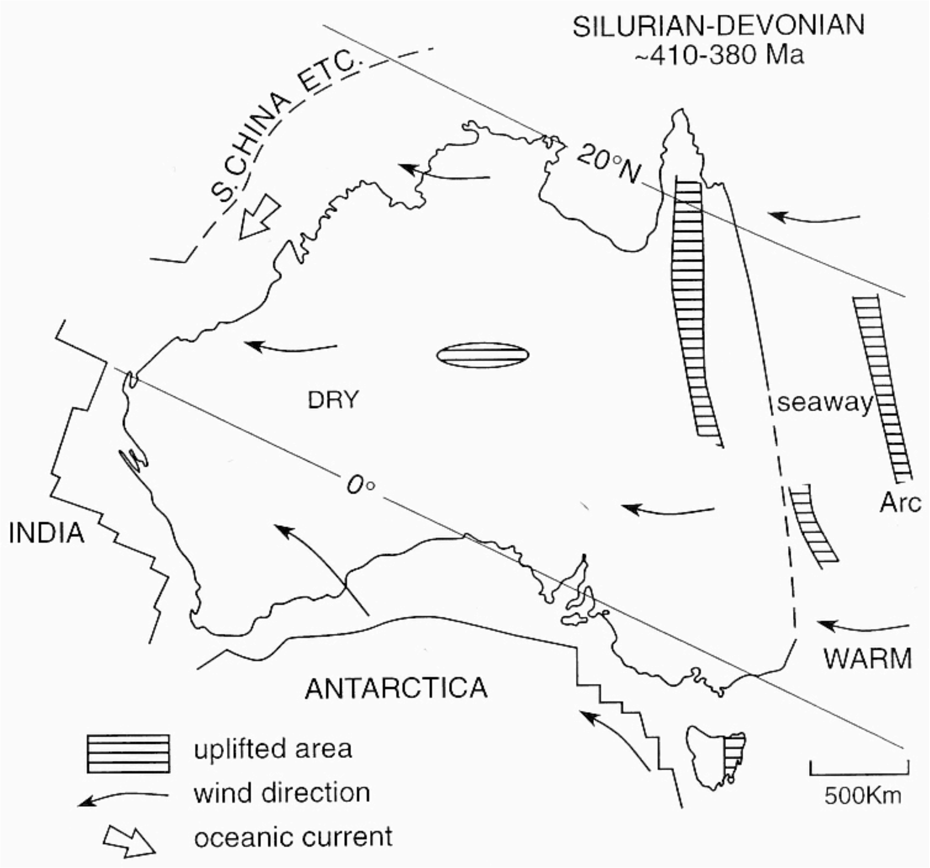

Figure 36. Tectonic uplifts and climatic elements of Australia, Silurian-Devonian (410–380 Ma). (Structures from Veevers *et al.*, 1991, and palaeolatitudes from Embleton, 1984).

The final isolation of Australia came about through a further major event. Beginning about 83 Ma, rapid seafloor spreading opened up much of the Southern Ocean south of Australia, albeit in the shape of a narrow seaway, and New Zealand and the Lord Howe Rise were isolated by spreading in the Tasman Sea (Fig. 38). The final stage in this sector was the separation of southern Tasmania and the South Tasman Rise from Antarctica at about 35 Ma (Veevers, 1988). Subsequent to these events, the only significant route for dispersal of immigrant plants over land was via bridges created during periods of low sea-levels in the Quaternary, on northern shelves connected to Papua New Guinea. Introduction of new taxa from nearby landmasses was also possible by wind and sea dispersal, but in a less predictable manner and probably to a lesser extent.

Topography

Elevation due to collision

Significant alterations to Australian landscapes resulted from tectonic activity associated with both docking of terranes and continental fragmentation. Uplifts generating erosion and sedimentary deposition in concurrently subsiding basins have been both localised relative to the surrounding countryside and continent-wide with respect to sea-level. In many cases the most conclusive evidence for uplift is found in basinal sediments, which can yield information about the provenance of the sediment and the direction, type and strength of transporting agents.

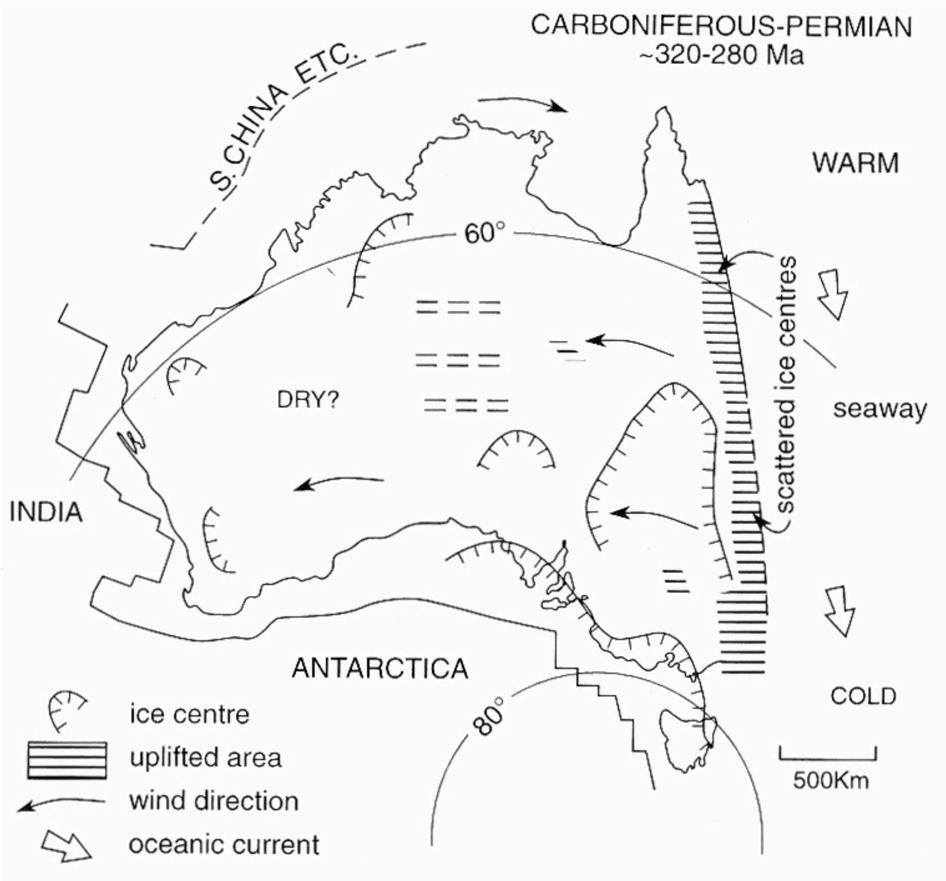

Figure 37. Palaeogeography and palaeoclimatic features of Australia at some time in the Carboniferous-Permian (320–280 Ma). (Structural framework modified from Veevers *et al.*, 1991, ice masses after Crowell & Frakes, 1975, and palaeolatitudes after Embleton 1984).

Little is known about the topography of Australia in the earliest Phanerozoic, but the Musgrave Block of central Australia underwent tectonic uplift in the Late Proterozoic and persisted as a mountainous area into the Cambrian. North-west marginal areas also demonstrate uplift in the Cambrian (Fig. 35). Cambrian docking of exotic terranes in the south-east no doubt raised mountains which only slightly later shed debris into newly created basins at their margins, as for example, the Melbourne Trough. Much of the remainder of the continent seems to have lain at a low elevation in this period.

The Late Cambrian Delamerian Orogeny (c. 495–515 Ma) raised highlands stretching from western Tasmania through the site of the present Flinders Ranges and on into north-eastern Queensland (Veevers & Powell, in Veevers, 1984). The Great Dividing Range of eastern Australia, on the other hand, owes much of its present elevation to the series of later collisional tectonic events as terranes attached themselves to the mainland during the Early Palaeozoic. The eastern highlands of Victoria and New South Wales and parts of Tasmania have undergone a series of denudations since about 365 Ma (Late Devonian), according to fission track dating by Foster & Gleadow (1993), Gleadow & Lovering (1978), Morley *et al.* (1981) and O'Sullivan *et al.* (1995). This dating is indicated by the length and density of fission tracks in apatite crystals in granitic rocks, which could only begin to form once the rock cooled to about 100°C. The cooling may have followed emplacement of the granite, or it may have resulted from intrusion-related uplift into cooler levels of the crust. Although uplift is implied in both cases, elevations cannot be specified. Throughout the first half of the Palaeozoic, mountain building/uplift in the eastern zone was accentuated by the construction of offshore magmatic (volcanic) arcs.

The Late Devonian–Early Carboniferous was a time of extensive vertical tectonics on the continent, and the effects lingered on into the latest Palaeozoic in the form of raised regional elevations (Fig. 37). In addition to the highlands raised in the eastern zone, uplifts also occurred in central Australia (Pertnjara Movement), where deformation continued at least to the end of the Early Carboniferous (Alice Springs Orogeny: c. 320 Ma). A substantial uplifted area thus reached from the central Northern Territory into north-eastern Western Australia, nearly to the Fitzroy Trough. Other smaller uplifts occurred adjacent to the Bonaparte Gulf Basin near the present coastline. Again, elevations of these uplifts cannot yet be specified, but it has been suggested that the region of the eastern margin was sufficiently high to initiate glaciation early in the Late Carboniferous (Crowell & Frakes, 1971; Powell & Veevers, 1987). A collisional episode of Palaeozoic uplift in north-eastern Australia carried over into the Early Triassic in the form of volcanic activity in east-central Queensland. Otherwise, the continent experienced a long interval of tectonic quiescence through most of the following Mesozoic Era.

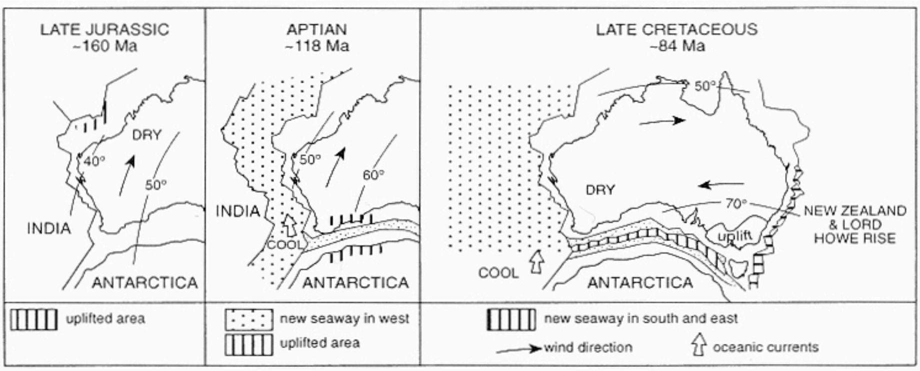

Figure 38. Palaeogeography, palaeoclimatic elements and the opening of the new ocean basins around Australia over the interval Late Jurassic to Late Cretaceous (160–84 Ma). (Modified from Veevers *et al.* (1991) with palaeolatitudes from Embleton, 1984).

At what stage New Zealand and the Lord Howe Rise attached themselves to Australia is not known precisely, but the event may be recorded in Late Jurassic magmatic activity along the New South Wales-Queensland margin. It is likely that this sector consisted of a series of blocks which were detached from the Antarctic landmass and moved northward along transcurrent faults.

Elevation due to marginal rifting

To this point, discussion has centred on Early to Mid-Palaeozoic land elevations created as a result of collisional tectonics, that is, by thickening of the crust due to opposed motions of 'core Australia' and other major blocks. Another principal means by which elevated topography is formed, doming of incipient continental margins by extensional forces, would also have been in operation over a long period of Australian history. The earliest such phase involved large scale extension and doming preceding the separation of the Himalayan and southern China blocks from the north-west margin (assuming that they actually were attached to the mainland in the manner suggested by Sengor (1987) and Veevers (1988); Fig. 38). As noted above, the precise timing of this event is uncertain but a post-Permian age is firm because the peripatetic fragments contain Permian stratigraphic sequences and fossil assemblages analogous to those of western Australia. The split-up probably took place in the Late Jurassic (post-Callovian, as suggested by Audley-Charles *et al*., 1988) concurrent with the earliest seafloor spreading, and may have occurred in two closely spaced stages, first southern China and then the Himalayan fragments. Preceding separation, it is likely there was doming in the region centred on the North West Shelf, followed by subsidence of elongate central segments (rifting). Eventually, the separated block moved laterally away from the new continental margin. Elongate domes, some also developing subsidiary rim basins, characterised the sites from which the now displaced Himalayan fragments departed. Similar uplifts of moderate altitude are likely to have occurred where later separations (i.e. of the Indian subcontinent, New Zealand-Lord Howe Rise, and Antarctica) were to take place (Fig. 38).

Fragmentation of the Australian sector of Gondwana thus led to the development of narrow and lengthy highlands which bordered a series of newborn rift structures around the periphery of the continent. Rifts and various associated rim basins vary in age from Callovian (Late Middle Jurassic; c. 160 Ma) in north-western Australia to probably about 55 Ma, when the Tasman/Coral Sea ceased spreading (Falvey & Mutter, 1981; Veevers, 1991b). Those bordering on the Indian Ocean proper propagated from the region of the North West Shelf and down the western margin in an anticlockwise fashion. Around the newly forming south-eastern margin, elevated rift shoulders and/or volcanic edifices were generated progressively from south to north as the locus of Tasman spreading shifted in the same direction into the Coral Sea. Elevated rift shoulders would have attained their highest relief at somewhat earlier times than those cited above. Elevations attained on rift shoulders are unknown, but the maximum might have been about 2 km, analogous to those reached in modern rift areas (east Africa, western North America). It is unlikely that such great heights were achieved in Australia, except possibly in the south-eastern highlands. However, elevations of about 1 km (Veevers & Cotterill, 1976) are considered reasonable estimates for many Australian rift shoulders.

The first rending of the Australian Gondwanan sector was at about 160 Ma, along the north-west coast of the continent (Fig. 38). According to Veevers (1984), uplifted blocks formed adjacent to the new ocean floor, but these lay well off the present coastline (200–300 km) and the continent was largely unaffected. Separation of the Indian subcontinent continued the process, with later rifting and drifting extending steadily southwards and then along the present southern continental margin. The Indian subcontinent was entirely freed from the west coast of Australia by c. 130 Ma. Uplift involving volcanism may have occurred near the south-western corner of the continent slightly before or during initial seafloor spreading there, at about 130 Ma. All such uplifts had subsided by the beginning of Tertiary time at 65 Ma.

Separation of Antarctica was preceded by a long interval of southern margin doming and rifting (Fig. 38) which finally culminated in the initial seafloor spreading and incursion of the sea into the Otway Basin at about 97 Ma. Volcanic activity accompanied rifting, as seen in volcanogenic sediments of the Otway Basin. However, the lack of volcanic centres of approximately this age along the margin suggests the sediments were derived either from horst blocks within the rift system or from the Antarctic side of the rift. Southern margin uplifts related to the south-eastern highlands are apparent in the fission track data cited above. These appear not to extend westward into the region of the Great Australian Bight, but do indicate that the highlands reached northward into central coastal New South Wales. It is probable that isolated uplifts existed along that section of eastern seaboard intersected by Tasman Sea/Coral Sea magnetic anomalies, that is, to latitudes matching that of the tip of Cape York. It is suggested that these uplifts were geographically distinct and were slightly older than the anomalies (again, beginning about 97 Ma and through to about 55 Ma); they were related to the series of rift structures that developed in marginal positions. The Tasman Sea/Coral Sea opening effectively removed New Zealand and the Lord Howe Rise from positions adjoining Australia and ended the extensional phase.

The lifespan for rifted domes, arches and other types of uplifts associated with extensional tectonics around the continental margins is speculative. The uncertainty is apparent from a variety of conceptual models which allow a duration of up to 50 million years for the interval from initiation of uplift to collapse, as signalled by the beginning of seafloor spreading. For our purposes, 30 million years is the span assumed in construction of Fig. 38. This is probably a sufficiently long time to allow migration of plants into elevated zones, for stabilisation of floras, and perhaps even for development of endemic taxa. The much more extensive lowlands, on the other hand, would have had a more diverse flora occupying a great variety of habitats across the continent. These are the taxa we can expect to be most common among fossil flora assemblages. However, vegetation in the lowlands, as in the highlands, was periodically exposed to influxes of plant taxa from adjoining landmasses and to marked changes in climatic conditions.

Evidence for past climates

Climate in Australia has varied over the last 570 million years. Changes have come about because of two main factors. Firstly, the continent has passed through climatic zones ranging from tropical to polar and sub-polar as a result of the motions of the Australian tectonic plate. Secondly, from an abundance of information it is known that the general thermal state of the Earth has undergone changes attributed to a variety of causes. At times, one or the other of these influences has been in the ascendancy, but the widest swings in the continental climate have resulted when the effects have been additive towards either warming or cooling.

Indicators of palaeotemperature

Most information on the history of Australian climates comes from studies on the biological content of ancient sedimentary rocks. These studies encompass all the modern techniques of palaeoclimatic analysis but unfortunately are concentrated in largely qualitative methods and on the materials formed in more recent times. As a result we presently have rather sketchy information on climates across the time spectrum and an abundance of data of somewhat limited scope concerning the last few million years. Perhaps it is because we have a relatively small ratio of scientists per km^2 of geology that the number of controversies is minimal.

Oxygen isotopes

The most powerful tool for the study of palaeoclimate is the oxygen isotope method, which uses the ratio of two isotopes to calculate the temperature of formation of carbonate minerals. These are frequently the product of shell formation by marine organisms and hence the past temperature of the marine waters in a basin can be determined. It can also be used on carbonates of non-marine origin, on the remains of fossil vertebrates such as reptiles and fish, and on other minerals, including clays. Surprisingly, given the presence of the necessary mass spectrometers and expertise at several institutions in Australia, the palaeoclimatic data gained by the oxygen isotope method are meagre when compared with those for most other continents.

Biological extrapolations

Other techniques, familiar to biologists, include determination of environmental parameters through studies of organic diversity and by estimation of past conditions through comparison of a fossil with a close living relative whose tolerances are known. Both methods, of course, have their limitations, in most cases related to uncertainties as to whether relationships between the organism and the environment have remained constant over time. Another commonly used procedure allows estimation of past climate parameters by statistical analysis of foliar physiognomy in fossil floras. The method relates the proportion of entire-margined leaves to the temperature and/or rainfall during growth of the plants by comparison with the leaf litter from modern floras (Wolfe, 1979). For Australian Tertiary floras, this type of analysis has some justification, as Australasian plants were considered in establishing the proportions among modern plant assemblages.

The first objective in many studies of fossil plants is to determine the environmental conditions of growth. Since few sites yield more than a few assemblages, it is not often that a record of any climate change at the site can be obtained. The situation then results in a scattering of sites of varying ages, not the best scenario for rigorous interpretation of climate history at a single site or of climate on a regional or continental scale. Ideally, a large amount of data from contemporaneous sites is required before meaningful interpretations of the variability of climate can be made for any sizeable area. Similarly, documentation of major climate change over time requires sequential data closely spaced in time and preferably from widely separated sites.

Rock types

The occurrence of certain rock types also is used to specify particular aspects of past climates. Particular strata are considered to have developed under similar conditions to those which developed their modern counterparts. Ancient climates are identified by making an analogy between rock type and modern environment; for example, the humid regimes of modern peat formation, the aridity of evaporite environments, the warm regimes of modern reefs and rainforests, or the frigid conditions which today feature in the formation of glacial deposits. Providing we know the full range of conditions under which distinctive sediments are formed, this is a valuable approach. Examples of past misconceptions include the idea that red non-marine sediments are restricted to arid conditions, and the notion that all limestones record warm water. Basinal conditions can be deduced from the distribution of some rock types, but the value of lithological indicators in palaeoclimatology is greatest when attempting to estimate the state of the climate on a global scale.

Indicators of humidity and aridity

Thus far, we have considered the means by which temperature can be measured or estimated. Temperature is an important parameter of the climate system and the one for which evidence is most easily obtained. Other aspects of past climate, such as precipitation and evaporation rates and wind speed and direction are more difficult to appraise, and atmospheric pressure of course is not recorded in sedimentary rocks.

Biological indicators

As mentioned, leaf proportions in foliar physiognomy studies can be used as a measure of humidity/aridity as well as for temperature estimation, but in some cases this can complicate the interpretation of temperature (Wolfe, 1977). The total composition of a flora or the presence of individual plant taxa having modern relatives of restricted tolerance can serve as guides to the annual or seasonal abundance of rainfall, particularly in Cenozoic assemblages. The width and character of growth rings in fossil wood is another important line of evidence from fossil plants (Chaloner & Creber, 1973).

Palaeosols

The type and thickness of palaeosols are reliable (although qualitative) indicators of past climate conditions and have been used extensively in Australia. Silcretes, calcretes, kaolinitic soils and lateritic profiles are abundant, and each carries its own significance as to mean annual rainfall and/or its distribution through the year. Palaeosols of Late Cenozoic age especially have been the subject of investigations, but their relative scarcity in older sequences limits their usefulness. Evidence for prevailing wind directions comes from the transport directions measured in rare occurrences of aeolian cross-bedded sandstones.

In summary, sedimentary rocks, including biogenic reef and other carbonate materials, are useful though not infallible indicators of warm climatic conditions. Tillites are the best indicator for polar/sub-polar climates, when identified by their association with other glacial facies. Between these extremes the assignment of palaeotemperatures on the basis of rock types is difficult indeed. Nonetheless, at times in the geologic record the distribution of variable lithologies provides a framework for palaeotemperature estimation. With regard to estimating precipitation, the chief indicators are the several ranks of coal deposits and their opposite numbers, the evaporitic minerals. Most studies of rock types for their palaeoclimatic significance have necessarily been limited to qualitative rather than quantitative results.

The sum of palaeoclimate data for the Australian Phanerozoic is disappointingly small. This limited information is summarised in the following sections and an effort is made to supplement it by projecting what is known of the history of the global climate state onto the map of the continent. Although most of what we know is concentrated in the later part of the geological record, the discussion follows the course of history, beginning at the opening of Phanerozoic time and proceeding through to the most recent past.

Chronology of Australian climate change

From the foregoing it is evident that there are many ways to estimate ancient climatic conditions. Such information, most of which is necessarily qualitative or semi-quantitative, can then be assembled into a history of climate. However, to summarise continent-wide data is to also generalise regional differences, thus blurring what might be significant variations from one place to another. A climatic chronology from the Cambrian to the end of the Cretaceous is presented in Fig. 39. In constructing the curves, trends in both temperature and precipitation are estimated for a point roughly located at the centre of the continent. The scales for both parameters are arbitrary and are meant to show only relative conditions.

Australia in the Early Palaeozoic: low latitude climates

Extensive Late Proterozoic glaciation of Australia (Adelaide and Flinders Ranges, Amadeus, Ngalia, Georgina and Officer Basins, plus the Kimberley region) ended a few tens of million years before the dawn of Phanerozoic time. In stark contrast, the initial Period of the Phanerozoic, the Cambrian, displays evidence of generally warm climates in the form of widespread carbonate strata deposited in a broad seaway spanning central Australia (Fig. 35). Many of these occurrences contain carbonate oolites or pisolites, which in modern environments are restricted to warm shallow seas. Structures resembling reefs and consisting almost entirely of archaeocyathids also occur in this region. Whether these grew in tropical environments typical of modern reefs, however, is uncertain owing to their great antiquity and lack of modern relatives. Attempts at oxygen isotope analysis of archaeocyathids have thus far proved unsuccessful, possibly because of internal variations in shell composition and diagenetic effects, whereby the isotopic composition can be altered by post-burial waters

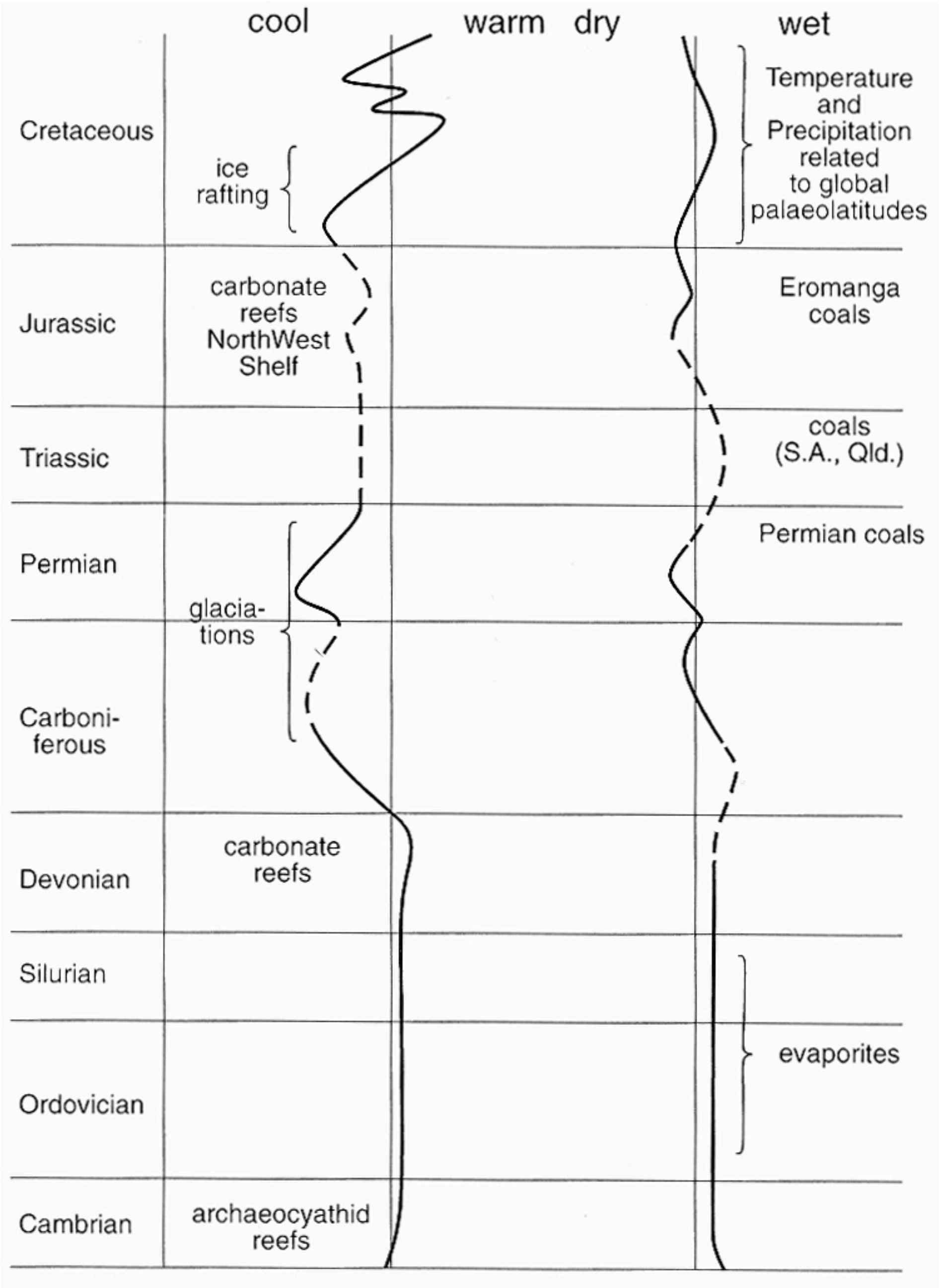

Figure 39. Estimated trends in palaeotemperature and precipitation for the centre of Australia. Note that the reference lines represent modern conditions. Arbitrary scales.

having different compositions. The available evidence, and the position of the continent, between about 5° and 40°N latitude suggests that Australia experienced a warm climate in the Cambrian. South-eastern regions, where extensional (South Australia) or collisional (mainly Victoria) tectonics were taking place, lay at the highest latitudes (Fig. 35) and may have experienced even cooler temperatures as a result of uplift, but direct evidence for this is lacking.

Northern Australia (Queensland, the Northern Territory and adjoining parts of Western Australia), located between about 10° and 30°N latitude and oriented so that it occupied a west-coast position at this time, was the site of non-marine evaporite and redbed deposition. As the precise longitudes of the southern China block are not known, the extent of any connection with Australia cannot be estimated, but we can speculate that there was a gap between the two landmasses possibly large enough at times for trade winds driving off the continent to create arid conditions similar to those which characterise modern west-coast deserts. In this scenario, the only source of atmospheric moisture was from marine basins in the interior; this, apparently, was not abundantly tapped and aridity prevailed in what is now the north.

In summary, the land area of the Cambrian continent was bisected by warm marine seaways and at least the northern one third of the continent suffered an excess of evaporation over precipitation. Most of the landmass experienced warm climates.

Climatic conditions during the Ordovician Period appear to have differed little from those of the Cambrian, judging from the deposition of carbonates and evaporites in the centre and north-west respectively (Fig. 36). Carbonates include coral reef structures that originated in docked terranes from the Pacific. Coarse clastic deposits in much of eastern Australia document the collisions of these fragments with the mainland and Tasmania and the elevation of highlands in the eastern quarter of the continent. As would be expected from its low latitude position, there is no evidence in Australia of the cooling and glaciation that affected the higher latitudes – northern Africa, central South America and parts of Europe – in the Late Ordovician and Early Silurian. Rather, essentially unchanged conditions since the Cambrian are in keeping with relatively slight changes in latitude (to within the band 20°N to 20°S in the Ordovician).

The Silurian and Devonian Periods, encompassing the initiation of significant terrestrial plant life, saw the passage of Australia out of the Northern Hemisphere and the early stages of a long journey to the polar zone. For most of this time, the continent remained between about 5° and 35°S latitude (Fig. 36) and, as before, with north-western Australia in a west coast orientation, trade winds passing over the mass of the continent would be expected to have led to aridity in northern and western areas.

Along with the disappearance of interior seas, regional changes in climate are well-documented for this time. For the Silurian, carbonate rocks containing reefal structures suggest warmth as might be expected from the east-west orientation of the continent. The reefs are found within the now-docked terranes constituting parts of Queensland, New South Wales and Victoria and thus lay facing the warm equatorial currents of the Pacific. In contrast, thick and extensive evaporite deposits of the Carnarvon Basin in Western Australia were deposited in a west coast position, adjacent to cool surface waters moving from higher latitudes. The Cambrian to Silurian saw a shift of evaporite environments from the north-east and north to the north-west of the continent in response to a clockwise rotation of some 90°.

It has been suggested that marked increases in the root mass (and biomass) of land plants in the Late Devonian led to a sequence of events as follows:

1) increased pedogenesis and stabilisation of landforms,

2) increased delivery of nutrients to the world's oceans,

3) increased marine fertility and burial of organic matter,

4) enhanced silicate weathering over the Earth, drawdown of atmospheric carbon dioxide, and consequent global cooling (Algeo *et al*., 1995).

The first Australian land plants appeared in Early Devonian time. The fossils are found in reddish sandstones suggestive of arid conditions in central and eastern Victoria.

Australia did not significantly change its position until late in the Devonian Period, when the Gondwana supercontinent began to accelerate its motion across the south pole. Although the clockwise rotation continued at a reduced rate, there was a perhaps unexpected shift in the distribution and a marked increase in the abundance of evaporite deposits. Evaporites formed in northern and central parts of the continent (Canning and Bonaparte Gulf Basins, Arckaringa Basin) and also expanded into the eastern regions (Adavale Trough of central Queensland). The latter possibly formed in a rain shadow of tectonically uplifted areas to the east, which sheltered the Adavale Trough from the moist Pacific trade winds. It is uncertain whether these deposits are all of the same age but most would fall in the Middle Devonian, a time of extensive evaporite formation on a global scale, perhaps because of major transgressions of the sea throughout the Period. Bauxites and other products of deep weathering did not develop in Australia during the Devonian, further supporting the idea that widespread aridity prevailed.

Carbonate strata also developed widely during the Devonian and carbonate reefs are found from Victoria to Queensland. The most spectacular occurrence is the Late Devonian structure at Bugle Gap in the Canning Basin, Western Australia. Reports of Devonian oolites are restricted to the Canberra region. However, the abundance of limestones is in keeping with the low latitude position of the continent and the global warmth of the Devonian. A cooling episode near the end of the Devonian led to short term glaciation in Brazil, but no indication of this cooling has been reported in Australia despite the motion of the continent towards higher latitudes. In summary, it appears that the low latitude warmth and aridity which characterised the Early Palaeozoic continued without significant interruption through into the Carboniferous. Aridity seems in fact have been more extensive in the Devonian than earlier.

Australia in the Late Palaeozoic: high latitude cooling and glaciation

Australia continued a rapid transit into the high latitudes in Carboniferous time, where it remained through the Permian Period, and as a result of its latitudinal position glaciation affected much of the continent (Fig. 37). In the Late Carboniferous and Permian, massive glaciation spread throughout much of the Gondwana supercontinent, but the earliest ice masses, as recorded by their deposits (tillites and associated strata), are located in eastern Australia and western South America. The oldest Australian occurrences, Namurian A in age (c. 330 Ma), are found in the Tamworth Trough and also near the coast east of the New England Highlands. They indicate the presence of glacial ice at sea-level, and thus extremely cold climates for this part of the continent. However, it is thought that the glaciers originated in elevated terranes and flowed downslope to form piedmont types adjacent to the sea (Crowell & Frakes, 1971). The remainder of the continent apparently was not affected by glaciation in these early stages.

It has been suggested that the Tamworth region and the elevated regions bordering on the Pedirka, Arckaringa and Cooper Basins of central Australia were glaciated as a result of contemporaneous mountain building known to have affected both the east and the centre at this time (Powell & Veevers, 1987). A difficulty with this idea is that the maximum age of the glacial deposits of central Australia has not been established and, although they may extend back well into Carboniferous time, they are dated only as 'Early Permian (Sakmarian) and older'. There is thus a gap of at least 45 million years between the timing of tectonic activity in the centre and the earliest dated glacial deposits in these basins. However, it is certain that glaciation and attendant cold climates were factors in the environments of central Australia by Early Permian time.

During the whole of the Late Palaeozoic (c. 360–245 Ma), Australia lay in latitudes higher than 25°S, but as a result of prolonged poleward motion, the whole of the landmass was positioned in the mid- to high latitudes (50–80°S) by the middle part of the Carboniferous. The near polar location of Australia and its neighbouring continents in Gondwana, thus provided seats for the growth of ice sheets, and no doubt made a major contribution to the most severe cooling recorded in Earth history. At no other time in the Phanerozoic was there such a congregation of landmasses in the polar zones and the coincidence in the Late Palaeozoic of polar landmasses and global cooling must be more than an accident of history. However, the development of large-scale glaciation seems to have taken a considerable time, as the deposits of the first Australian ice sheet (Late Westphalian, c. 300 Ma) post-date those of the mountain and piedmont glaciers of eastern Australia by at least 20 million years. Dating for an ice sheet which covered much of the east, from Tasmania to Queensland, is uncertain, as it is derived from the apparently long-ranging *Potonieisporites* palynoflora (Late Carboniferous to Early Permian). A second ice sheet occupying parts of South Australia originated from adjacent Antarctica. Tillites there record glaciation near sea-level, but the timing (Latest Carboniferous to Early Permian) is similarly obscure. Considering the global range of ages cited for the Late Palaeozoic glaciations, Frakes *et al*. (1992) suggested that the relatively few citations for the Latest Carboniferous is evidence that there was a warming within the major Late Palaeozoic glacial interval, a possibility supported by Crowley & Baum (1992), despite calculated low atmospheric carbon dioxide levels.

The Early Permian (Asselian-Sakmarian (290–269 Ma)) saw the greatest expansion of ice on the continent, with glacial deposits laid down as far north as 60°S latitude (Fig. 37). An amalgamated ice sheet spread over the present east coast from southern Tasmania to as far north as central Queensland and stretched to the basins of central Australia. Separated centres for the growth of ice also existed in the west, next to the Perth, Carnarvon, Canning and possibly the Bonaparte Gulf Basins. For these, the geographic extent of the ice cannot be determined due to subsequent erosion or deep burial of the deposits, but ice masses do seem to have been limited geographically. Judging from the nature of the deposits, the intensity of cooling may have been substantially less than in the eastern centres. The central basins lay in a broad belt of high latitude westerly winds which, after their long passage over the continent, were relatively dry. There was also a shortage of moisture sources for ice growth within the centre, as the few marine basins there would have been frozen over for much of the year. The restricted growth of the ice masses of the Australian centre was probably regionally related to elevated terranes raised during Early Palaeozoic tectonism. Over this time interval, while the continent lay in roughly the same orientation as now (i.e. with its long axis roughly parallel to lines of latitude) only the far north of the continent experienced moderate temperatures. Migration of those land plants requiring a land connection was severely constrained in the Early Permian because of the ice, and only hardy immigrants (*Glossopteris*? etc.) would have arrived, probably from the Indian subcontinent to the west.

Vegetation patterns during the Sakmarian (c. 275 Ma) were reduced to biomes by Ziegler (1990), who interpreted them to indicate a variety of climate conditions:

far north	temperate evergreen forests	warm temperate, humid
north-west	tropical deciduous forests	tropical, humid summers
south-east	(boreal) coniferous forests	cold temperate
south	–	ice-covered, polar

In the Late Permian, the gradients in temperature south to north across the continent averaged about 20°C, according to the modelling results of Fawcett *et al*. (1994). There were strong seasonal variations with winters averaging between -10°C and +10°C and summers between +10°C and +30°C. The coolest region was located in the south-east.

The frigid landscape of Australia, along with the remainder of Gondwana, warmed greatly toward the end of the Permian Period. This took the form of increased seasonality, as seen in computer climate modelling and comparisons with the vegetation biomes of this time (Kazanian, see Kutzbach & Ziegler, 1994). From inferred vegetation biomes, Ziegler (1990) predicted that most of Australia was covered by cool temperate broadleaf (nemoral deciduous) forest during the Kazanian. Temperatures in the centre in mid-summer reached 35°C and in winter -15°C. The geological evidence tells us that most continental ice had melted abruptly by about 269 Ma (end Sakmarian). Tasmania appears, quite understandably considering its southern position, to have been the last region to come out of the cold spell. The evidence, however, does not support the presence of a late ice cap there, but instead signals the final decay of the ice masses during a time of strongly seasonal climates, which included winter freezing to form river and marine shore ice at basin margins. Ice floes carried stones northward into marine environments in Tasmania and along the southern New South Wales coast and deposited them during summer melting. The same process began and ended in eastern Queensland somewhat earlier. As a result of general global warming ice rafting had ended in Australia (and in conjugate Siberia, the only Northern Hemisphere locality where the process has been identified), and in Gondwana, by about 250 Ma.

A major problem is posed by the termination of both the extensive glaciation of Australia and the subsequent seasonal ice rafting while the continent maintained a polar to subpolar position. At this key time there is a lack of climate indicators to support the climatic conditions suggested by the latitudinal position of the continent. It appears that a major shift in the state of the global climate led to substantial warming at all latitudes in the Late Permian. The forcing function for warming probably lay in the geochemical cycle of carbon. A geochemical model relating the consumption of carbon during the weathering of silicate rocks to global tectonic events and sea-level (Berner, 1994) reveals that the drawdown of atmospheric carbon dioxide was very strong from the Early Carboniferous until the middle Jurassic. This can satisfactorily explain the cool Earth of the Late Palaeozoic mainly as a consequence of tectonic activity, but not the termination of glaciation nor the warm and wet conditions, characterised by the deposition of the later Permian coals in New South Wales, Queensland and Western Australia, which followed. One hypothesis to address this warming suggests the release of carbon dioxide from ocean waters and seafloor sediments to the atmosphere near the end of the Permian (Frakes *et al.*, 1992).

Some climate modelling also suggests the initiation of monsoonal conditions in Late Permian Australia (Kutzbach & Ziegler, 1994). These monsoons were felt most strongly in eastern Australia, where rainfall varied from more than 2000 mm/yr in summer to about 1000 mm/yr in winter. Monsoonal conditions originating at this time extended into the Triassic, when they dominated the climate over a large part of Gondwana. However, modelling by Fawcett *et al*. (1994) suggests high summer rainfall in the west and south-east but only moderate rainfall (c. 1000 mm/yr) for most of the continent.

The cooling of Gondwana during the Palaeozoic was a major event in the evolution of Australian environments. However, the long transition from tropical to sub-polar regimes, reflecting the drift to high latitudes, brought about gradual rather than sudden change. Consequently, the stepwise impacts on the fauna and flora of the continent, although dramatic in the long term, were subdued over short periods. In this sense, Australia, particularly the western part, may have acted at times as a refuge for life forms of Gondwana but it was not the sole location from where re-establishment of stocks throughout the supercontinent could occur. Although northern parts of Africa and South America, possibly cooled, they were not subjected to glacial conditions, and other regions underwent only sporadic spells of glaciation. As long as intercontinental connections survived beyond the ice sheets, so too could the Gondwanan biota.

Australia in the Mesozoic – a totally different picture

During the Mesozoic Era (the Triassic, Jurassic and Cretaceous Periods), Australia remained in the high latitudes (Fig. 38), yet the only indication of cool climates is found in Early Cretaceous strata of the centre (Fig. 39). The abnormal warmth which began late in the Cretaceous is documented in all continents and signals a global warming which is unprecedented in Earth history.

Triassic

The Triassic Period saw a concentration of the world's landmasses across the equatorial zone and the consequent development of widespread monsoonal conditions (Robinson, 1973; Parrish *et al*., 1982; Frakes *et al*., 1992). Australia, however, was positioned too far south to be affected by tropical monsoons. Rises in global sea-level were associated with the melting of the ice in the Late Permian but, paradoxically, during the Triassic interval of warmth there was a withdrawal of the sea from all around Australia. This latter observation seems a contradiction in itself, as an Earth without polar ice caps would be expected to experience rising sea-levels as water from melting polar ice returned to the oceans. The alternative mechanism for global lowering of sea-level may resolve the difficulty. Decreased tectonic activity in the ocean will lead to increased volume of the ocean basins and hence, regression of the sea from continents. There is no model of continental evolution which would permit the opposite mechanism, a comprehensive rise of the continents. In the Triassic Period, the only slight encroachments of the sea onto the land were in southern coastal Queensland and the Perth and Canning Basins, where previously formed basins already existed. In general the landmass appears to have been without large scale relief, except perhaps in near-coastal zones of northern New South Wales and Queensland where tectonism and associated volcanism took place in the Early Triassic (c. 245–241 Ma).

Paradoxically, at the time Australia lost its glaciers, the continent moved into yet higher latitudes. During the Triassic the pole appears to have moved into south-eastern Australia (Fig. 33) and at no time in the period did the continent extend to lower latitudes than about 55°S. Did the pole move or the continent? The fact that Triassic polar Australia underwent significant warming and lacks any evidence of glaciation whatsoever is but a part of the bigger problem – the total lack of any glacial evidence on the globe at this time, the only Period in the Phanerozoic for which glaciation is not documented.

Quantitative estimates of Triassic temperatures (from oxygen isotope studies) are few in number and restricted to the Tethyan low latitudes (Hudson & Anderson, 1989). As a result, the Triassic thermal state of Australia is poorly known. Some suggestion of aridity in the Early Triassic is offered by red shales and sandstones that occur in small patches around Australia, but further studies are required to substantiate the idea that the coloration represents oxidation during deposition, as seen in some modern deserts. The best indications of Triassic climate come from the coals of small basins within the Flinders Ranges of South Australia, in Tasmania, and also from the coastal regions of New South Wales and Queensland previously affected by volcanism. During the Middle and Late Triassic (about 241–208 Ma) these regions became centres for humid climates, which may have been of much greater extent. The east coast deposits can be explained by their location: as in previous glacial times, warm currents moving southwards from the equatorial Pacific would have provided these areas with abundant precipitation (Fig. 37). Retallack (1977) has interpreted Triassic palaeosols of the Sydney Basin as indicating a cool-temperate climate, and similar conditions have been suggested for the Bowen Basin, Queensland and south-eastern Australia (Townrow, 1964; Jensen, 1975).

The recent development of mathematical models of the climate system now allow simulations to be made of past and present climates. The General Circulation Models (GCM) lack fully linked oceans and suffer from other imperfections, but even with these limitations they can provide clues to forcing functions and the state of the climate in times past. Following attempts using conceptual models (e.g. Robinson, 1973; Parrish *et al*., 1982), Kutzbach & Gallimore (1989), Fawcett *et al.* (1994) and Pollard & Schulz (1994) investigated Triassic climates with a GCM under several scenarios. Fawcett et al. (1994) found extreme winter temperatures of less than -30° warming to +10°C in summer in the south-east, coincident with suggested high topography. The 0° isotherm extends nearly to the north coast in the Late Triassic in winter. The previously suggested monsoonal conditions in low latitudes were supported by the results, but high rainfall was also indicated for regions beyond about 35°S latitude. The segment which includes all of Australia at this time experienced precipitation in excess of 550 mm/yr; except for rather small areas in the centre and the far north, there was a positive precipitation minus evaporation balance, in keeping with most geological indicators. Regarding temperature, the model gave latitudinal ranges for summer of 15° to 25°C and winter of about 10° to -30°C, suggesting strong seasonality and continentality.

Jurassic

The Jurassic Period, like the Triassic before it, has few climatic indicators. During this time Australia briefly moved to slightly lower latitudes (range from c. 35–65°S, Fig. 38), before reversing its course in the Early Cretaceous. Again, despite its location in relatively high latitudes, there is no evidence for glaciation in Australia, although probable glacial deposits have been reported from adjoining Antarctica (Woolfe & Francis, 1991). Glaciation has not been reported elsewhere at this time, although seasonal ice rafting probably took place in high latitudes of Far-Eastern Siberia during the Middle Jurassic (Chumakov & Frakes, 1997).

Sea-level remained low, with the consequence that marine embayments were restricted to parts of the Perth, Carnarvon and Canning Basins in the west. A major palaeogeographic development was the initiation of the great interior lowland which still persists today, the Great Australian Basin, at this stage better known to palaeogeographers as the Eromanga Basin (Krieg *et al*., 1995). Accumulation here was primarily in the form of fluvial sediments of a large sandy river system draining to the east, but thin and discontinuous coals, indicating an excess of precipitation over evaporation, were common here and in coastal areas of Queensland. These indications of humidity, as before, can be attributed to the persistence since the Late Palaeozoic of proximal warm currents derived from the western Pacific. Hallam (1985) suggests that coal-delineated wet climates extended farther west and north to encompass most of Queensland and New South Wales in Late Jurassic time. The east-west orientation of the north-western continental margin would have favoured the initiation of seasonal monsoonal precipitation there. However, the only sedimentological information from that region comes in the form of fluvial deposits which lack coals or other indications of a wet climate.

Numerical modelling of past climates using General Circulation Models has now been applied to the Jurassic (Chandler *et al.*, 1992; Moore *et al.*, 1992; Valdes, 1994; Fawcett *et al*., 1994). Chandler *et al.* (1992), on the basis of qualitative evidence of mean global zonation, set boundary conditions for the model by assuming Early Jurassic sea surface temperatures (SSTs) of 14° and 9°C off northernmost (Darwin area) and southernmost Australia (Tasmania), respectively, and relatively subdued topography throughout the continent. Slight elevations are assumed for eastern Queensland. These and other inputs to the model for this time enabled the model to reach stability. One could conclude therefore that the use of these specified temperatures was justified, and that they provided an approximation of Early Jurassic conditions. Continental temperatures, which were not specified but instead produced by the model, showed moderate summer-winter variability (Darwin 10° to 19°; Tasmania -12° to 10°C) and zonal arrangement of isotherms. Despite the success of the simulation in some respects, the model cannot address the problem of how high temperatures can be maintained at high latitudes. Finally, the model indicated generally low positive values for precipitation minus evaporation over Australia, more or less in keeping with the known distribution of coals.

Mid-Jurassic climates were simulated by Fawcett *et al*. (1994), who found that Australian conditions had warmed considerably since the Late Triassic. They defined the climate as generally humid, warm temperate to subtropical, with a mean annual temperature range of about 30°C and rainfall totalling an average of about 1500 mm/yr. Rainfall was heaviest in the continental centre.

Moore *et al*. (1992) utilised a GCM to investigate the Late Jurassic. Their boundary conditions included increased levels of atmospheric carbon dioxide (at 1120 ppm, about 4 times the present level) and topography to 2 km elevation in coastal eastern Australia; both SSTs and continental temperatures were determined by the model. Winter to summer temperatures were calculated to be about -10° to 20°C for Darwin and -22° to 10°C for Tasmania, and winter sea ice would have formed off eastern Australia at this time. Annual precipitation was estimated to have been greater than 1000 mm/yr except for the south-east (where some of the Australian coals occur), but north-eastern Australia showed the greatest excess of precipitation over evaporation anywhere on the Jurassic globe. Storms would have affected the north-west of the country, as the axes of mid-latitude storm tracks trend from Darwin to North West Cape. Here, wind strengths above 60 km/hr would have been common.

The Valdes model of Late Jurassic climates (Valdes, 1994) assumed similar SSTs as estimated by Moore *et al*. and arrived at similar conclusions.

General Circulation Models are known to be imperfect in their attempts to simulate both present and past climates. But from the above results it can be said that increased carbon dioxide in the atmosphere contributes to relatively warm summers, which in turn suppresses the formation of permanent ice masses at the poles. Accordingly, although winter freezing was common in the centre, glacial deposits are not to be expected in the Australian Jurassic high latitude sites. Also, Jurassic coals appear to be fairly reliable but not precise indicators of high precipitation and excess precipitation over evaporation, and, in the case of Australia, this leads to the conclusion that the north and west of the continent experienced humid climates (rainfall of perhaps as much as 1300 mm/yr), while over the remainder of the continent precipitation was lower and there was an approximate balance between precipitation and evaporation. The Australian monsoon, which had its origins in the Late Permian, seems to have terminated within the first half of the Jurassic. As today, storminess seems to have been a feature of northern Australia, and the roughly east-west orientation of the north coast would have been conducive to monsoonal activity. While the geological information available to define Australian Jurassic climates is meagre, it is sufficient to sketch the general picture which can then be filled in by modelling.

Cretaceous

The climates of the subsequent Cretaceous Period (c. 145–65 Ma) are even more complicated, showing a greater degree of variation because Gondwana was beginning to divide. This created new seaways, which helped to moderate continental climates and provided new sources of moisture for evaporation and precipitation. The most significant separation, in terms of Australian climate, seems to have been the drifting away from Antarctica, which occurred in the Albian (112–97 Ma), as documented by the earliest marine sediments of the new seaway in the Otway Basin. Several lines of evidence indicate that Australia during the Cretaceous was characterised by surprisingly cool climates in the first half and warmer conditions thereafter. Also important for climates was the movement of the continent into higher latitudes. From the Valanginian (c. 140–135 Ma) to the Early Albian the bounding latitudes were between about 45° and 80°S, the highest they had been since the Late Palaeozoic. The Cretaceous also saw what were probably the highest sea-levels on record for the Phanerozoic (Turonian, c. 90–88 Ma; Haq *et al.*, 1987) and the creation of an extensive seaway occupying the central lowland areas. The lifetime of this continent-bisecting seaway almost precisely coincided with the duration of the first half of the Cretaceous (c. 145–97 Ma), and throughout its existence it would have hindered the spread of land plants.

The evidence for cool conditions in the Early Cretaceous comes from several sources. Palaeontological and oxygen isotope data from the Aptian–Albanian of the Otway Basin are interpreted as signals of temperatures near zero (Rich *et al.*, 1988; Gregory *et al.*, 1989; Ferguson *et al.*, 1993). Strata of Valanginian to Albian age (c. 140–110 Ma; Alley, 1988) contain coarse clasts to boulder size, which apparently were dropped by melting ice floes into marine muds of the Eromanga and Carpentaria Basins (Frakes & Francis, 1988; Frakes *et al.*, 1995). This interpretation was first put forward by Brown (1894) and, after some alternative ideas were discarded, supported by David (1950). Because evidence of glaciation in the form of tillites is not present among Australian Cretaceous strata, ice floes formed in winter and melting in summer, as opposed to icebergs from glaciers, are preferred as the agent of rafting of the coarse material. Therefore, the suggested climate, at least for eastern Australia, is a strongly seasonal one which also included frequent storms, judging from sedimentary structures. GCM modelling results indicating an annual temperature range of about 45°C (between c. 27° and -18°C) for central Australia support such a view (Barron & Washington, 1982).

A second powerful line of evidence comes from oxygen isotope analyses of Late Aptian glendonites from the Eromanga Basin. Preliminary study of these stellate calcite pseudomorphs of ikaite, a cold-water carbonate mineral, demonstrates low salinity for the

Eromanga seaway, thus permitting calculation of palaeotemperature of bottom waters using a new value for the isotopic composition of high latitude oceans (De Lurio & Frakes, in prep.). Previously determined bottom water palaeotemperatures from the Eromanga/Carpentaria by the isotopic method on carbonate fossils (Dorman & Gill, 1959), when recalculated on this basis, yield values of generally less than 10°C. Thus this work indicates the presence of a seasonally cold seaway in the centre of the continent in the Early Cretaceous, which probably derived ice floes and large quantities of cold fresh water from highland sources lying to the south and east of the basin. The highland source is supported by other evidence. Frakes & Francis (1990) and Francis & Frakes (1993) showed that growth rings in Eromanga fossil araucarian and podocarp wood indicated both a lowland population displaying relatively broad rings and a highland group with narrow rings. It was pointed out that the first group had modern counterparts in warm- to cool-temperate forests of Australasia, while features of the second population were closer to those of trees from cold-temperate regimes of the western slope of the Patagonian Andes. The coastal ranges of south-eastern Australia were the likely source of the narrow-ringed wood types and the climate conditions there can be considered as analogous to those of Patagonia. Snowfields in this region also supplied the abundant fresh water which fed the Eromanga Basin and the ice floes, probably from rivers which underwent winter freezing. Still farther south, in the Otway Basin, meltwaters have also been suggested to explain large negative values of oxygen isotopes and low temperatures (-5° to 5°C) from carbonate concretions of Aptian-Albian age (Gregory *et al.*, 1989). A different explanation for these results is offered by Spicer & Corfield (1992). Palaeobotanical data (Parrish *et al.*, 1991) provide a MAT estimate of 5–8°C for the Albian of the south-east, somewhat at odds with the isotopic and other estimates. However, it must be remembered that because stratigraphic control is poor (Dettmann *et al.*, 1992), such 'inconsistencies' might be merely reflecting sharp climate fluctuations on time scales of 1 million years or less.

At this time the continent possibly had three climate zones (Frakes *et al.*, 1995). Beyond c. 72°S palaeolatitude, in the south-east of the mainland and probably including Tasmania, highland terranes suffered very cold winters but somewhat warmer summers causing much melting of snow. Between c. 72°S and c. 53°S rafting by river ice into marine basins affected the Eromanga and Carpentaria Basins, signifying strongly seasonal climates and bottom waters with temperatures less than c. 10°C. Beyond c. 53°S palaeolatitude, the climates were warmer and seasonality was less marked. From Fig. 40 it can be seen that the western half of the continent lay within this warmer zone.

The foregoing discussion relates primarily to the time most closely identified by the age of the Eromanga glendonites which have been studied, and not to the whole of the Valanginian to Albian interval in which dropstones occur. In fact, the sporadic distribution of the dropstones and the glendonites in Australian Cretaceous basins is more suggestive of fluctuating temperatures. It is likely that climates alternated between the Late Aptian conditions described above and more equable climates. However, this has not been confirmed, because of a lack of suitably dated sequences showing obvious cyclicity.

Australian palaeoclimatic conditions can be estimated in more detail, although not necessarily with more accuracy, by examining global temperature variations as a function of latitude and time. It is assumed, firstly, that temperature data from around the world can give a reasonable picture of global climate evolution, and secondly, that this averaging technique can then be applied in estimating the thermal history of Australia as it moved across lines of latitude. Continental and oceanic temperature data from a variety of sources yield the picture seen in Figs 41 and 42 respectively (Frakes *et al.*, 1994; Frakes, submitted). Isotherms swing towards the high latitudes at times of warming and towards the low latitudes when cooling is underway. For Australia, which occupied the space/time belt between the heavy lines, it can be deduced that the Early Cretaceous was a cool time with mean annual temperatures near freezing over a large part of the continent. However a warming, in part reflecting the acceleration in Australia's northward motion, was in progress. By the end of the Albian (c. 97 Ma) the 0° MAT isotherm lay along the southern margin of the Eromanga Basin and only the far north of Australia experienced MAT above 10°C, according to GCM modelling by Barron *et al.* (1995). This modelling experiment included a 30% increase in the

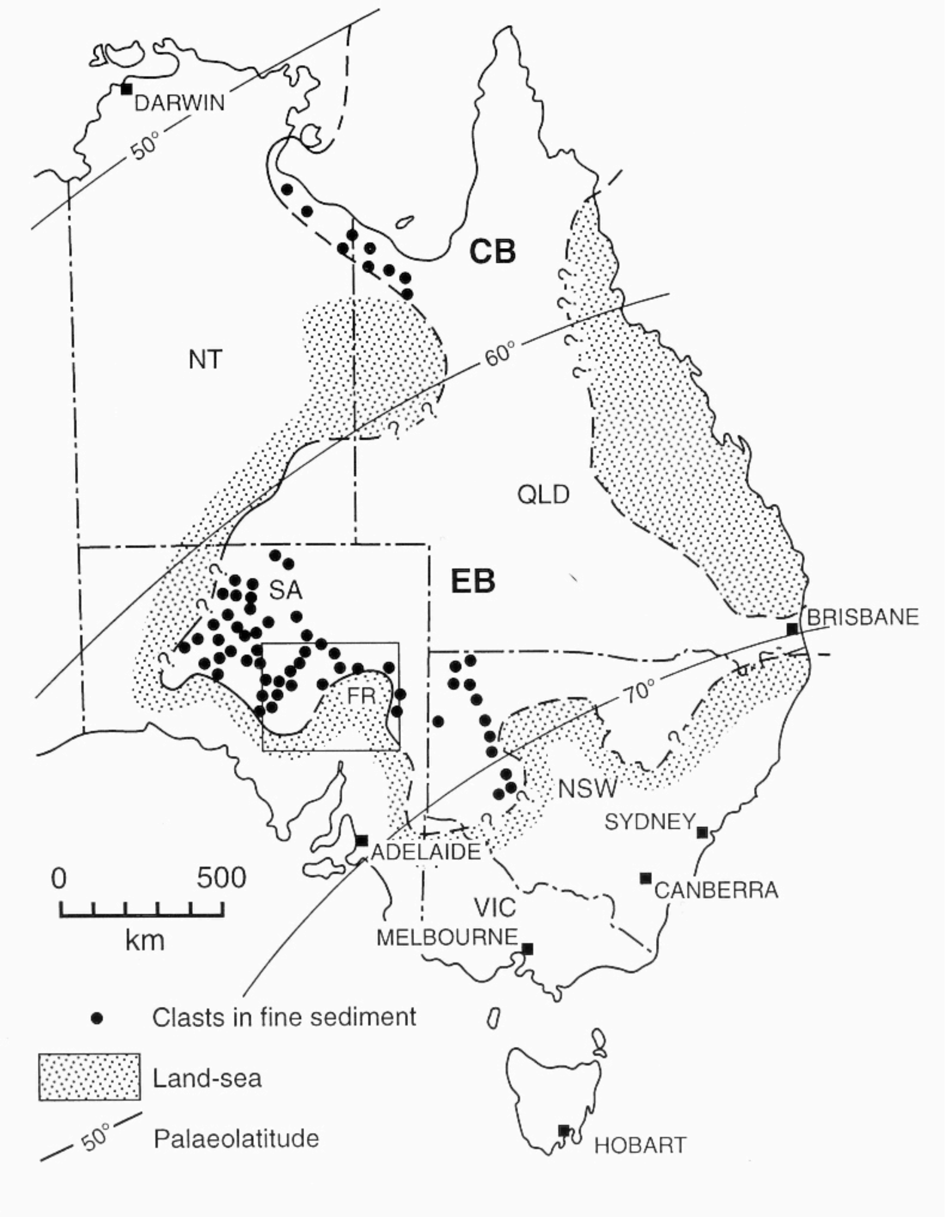

Figure 40. The distribution of ice rafting and the climatic zonation of eastern Australia during the Early Cretaceous. EB= Eromanga Basin, CB= Carpentaria basin. (Modified from Frakes *et al*., 1995).

transport of heat by the ocean relative to the present, and a carbon dioxide level four times that of the present. The Turonian (c. 90–88 Ma) seems to have been the time when warming peaked, with MAT for Australia of about 13°C in the south and 23°C in the north of the continent. One result of this warming was the coincident extreme peak in global sea-level. Douglas *et al*. (1976) suggest that Victorian plant fossils suggest cool climates which continued until the Santonian (c. 86–83 Ma), but the global data indicate cool conditions persisted until the Maastrichtian (c. 74–71 Ma). The closing of the Cretaceous (c. 65 Ma) witnessed a short sharp warming followed by a marked cooling at the opening of the Tertiary Period.

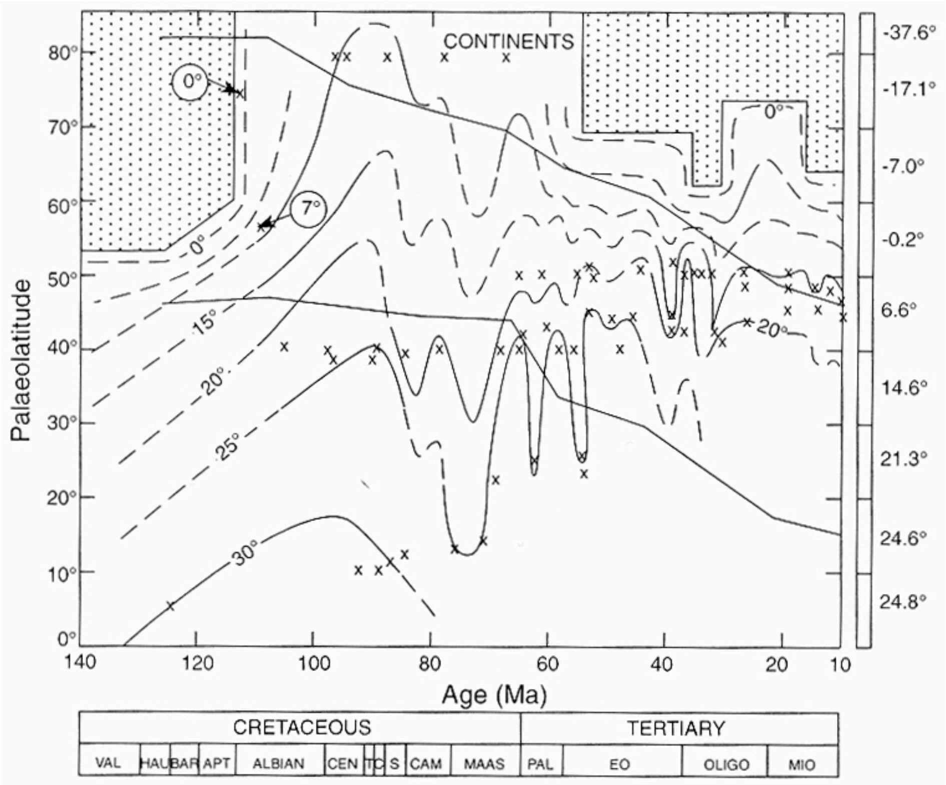

Figure 41. Space/time plot of published global palaeotemperatures for continents, Cretaceous to Middle Miocene. Note that both Hemispheres are included. The hatched boxes represent the distribution of known ice rafting and the numbers along the right margin are mean surface temperatures for each 10° latitude band at present (Willmott & Rowe, 1985). The diagonal lines represent the northern and southern extremities of Australia. (Modified from Frakes *et al*., 1994).

It is known that the global climate fluctuated in the second half of the Cretaceous (post-97 Ma), but such changes are not well documented in Australia because of a general scarcity of data. The interior seaway had dried up and there were only minor incursions of the sea onto the continental borders. A major warming effect was felt on the North West Shelf of Australia, where clastic sedimentation was replaced by the widespread accumulation of carbonate sediments. This occurred approximately in the Turonian, a time of warming in the world oceans (Fig. 42), and carbonates have continued to form there up to the present. It has been suggested that conditions were warm enough for carbonate minerals originating largely as shell materials of marine organisms to be preserved from dissolution. It is possible that formation of Late Cretaceous carbonates of the North West Shelf benefited from relatively warm surface waters diverted southward from the equatorial currents. It is also possible that these mid-latitude carbonates are of the temperate carbonate types which can form in comparatively cool conditions, but this has not been investigated.

Precipitation is an often ignored aspect in palaeoclimate studies, partly because it is often difficult to separate precipitation from temperature effects but also because what is likely to be preserved in fossil and sedimentary materials reflects the balance between precipitation and evaporation. The abundant Australian palaeosols, although potentially of value, provide few opportunities for determining precipitation rates because they are poorly dated, some as Early or Mid Mesozoic, others as pre-Late Mesozoic or even Permian (Bird & Chivas, 1989; Benbow *et al.*, 1995a). Studies of leaf morphology and palaeo-ecological comparison with nearest living relatives has sometimes been of use. However, given the vast differences between Cretaceous plants and modern forms, such approaches have not always been wholly reliable in estimating past rainfall. Yet, on the basis of Eromanga Basin palynology and sediment types, Krieg *et al.* (1991) and Benbow *et al.* (1995b) suggest humid climates for the south of the Early Cretaceous Eromanga Basin, and Evans (1967) considered that thin Late Albian coals near Nhulunbuy in the Northern Territory indicated abundant rainfall there.

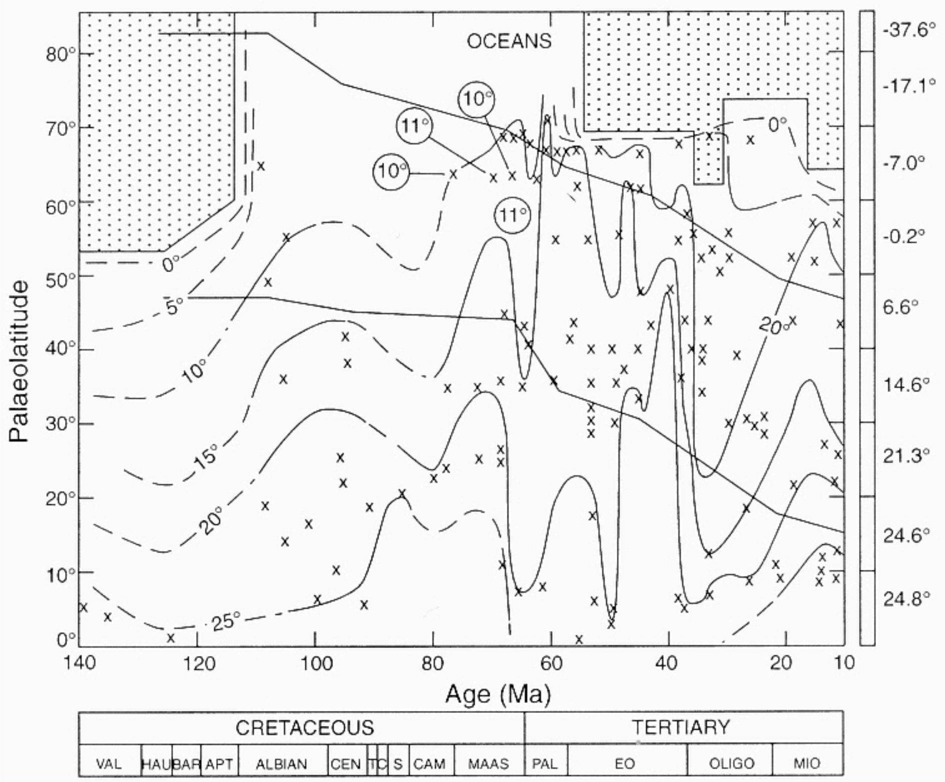

Figure 42. Space/time plot of published palaeotemperatures for world oceans, Cretaceous to Middle Miocene. Hatched boxes and diagonal lines are as in Fig. 41 and numbers on right are mean sea surface temperatures for 10° latitude bands (Shea *et al.*, 1990). (Modified from Frakes *et al.*, 1994).

Others have favoured widespread low-latitude aridity (to c. 45°S latitude in Africa and South America) on the basis of fossil floras and evaporites from the Aptian (c. 124–112 Ma), a time when the equatorial humid zone apparently did not exist (Chumakov, 1995). The latter study also suggested that a humid tropic zone came into being in the Albian and extended until at least the Cenomanian.

An alternative method of estimating, and perhaps predicting, palaeoprecipitation relies on the global relationship between precipitation and temperature (Fig. 43). From this information, it can be stated that MAT less than 20°C corresponds on average with precipitation of less than 500 mm/yr, and MAT of 25° generally leads to rainfall of more than 1580 mm/yr. These isotherms, from Fig. 41, can thus be taken as defining precipitation rates and are plotted on Fig. 44. Interpretations from this method do not take into account the possibility that unusual circumstances (coastal oceanic currents and upwelling, regional orographic effects, continentality) may have caused substantial deviations from the global norm, and indeed, such deviations are well known among modern climates. Assuming strict conformity with the globally averaged conditions, the results suggest that Cretaceous Australia was mostly semi-arid, except for northern regions near the temperature maxima (Albian to Turonian; c. 112–88 Ma, and Late Maastrichtian, c. 70–65 Ma). This dryness is surprising because throughout the Cretaceous Australia lay with the northern margin in east-west orientation (at c. 45–50°S latitude), in a situation where a seasonal monsoon might have developed. It seems that only in the Albian–Turonian interval and the Late Maastrichtian were conditions in the north entirely suitable for monsoons. It appears that the whole of Australia occupied a cool dry zone until the Albian.

Palaeogeography also played a role in setting the Australian climate during the Cretaceous. Most important were the predicted tracks for the polar easterly winds, which would have blown strongly across the continent from what are presently the east and north-east (Fig. 38). These winds, first moving over the cold seas beyond New Zealand and then over the breadth of the continent, would have been mainly dry, and any available moisture would have been precipitated on the elevated terrain in south-eastern Australia, thus leading to the formation

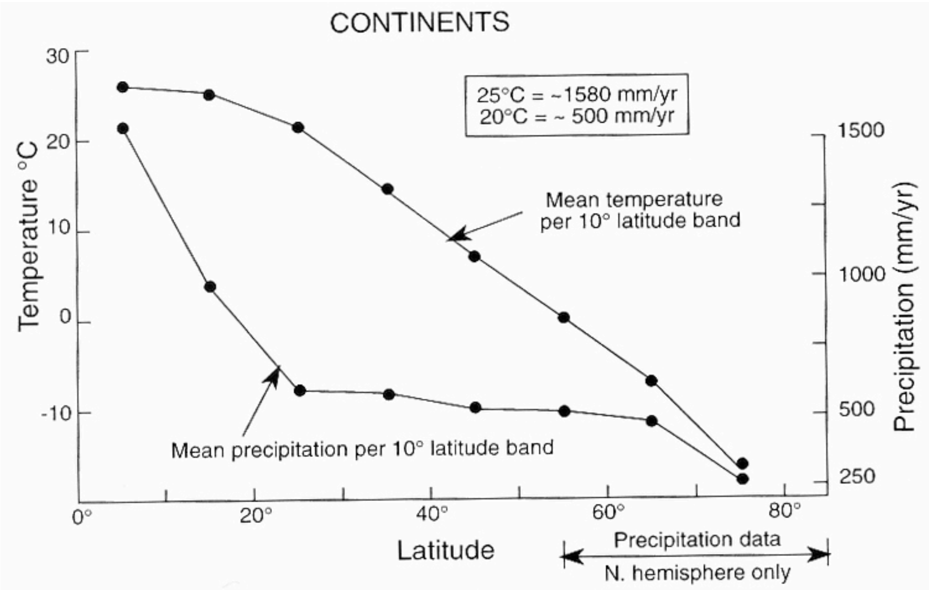

Figure 43. The global relationship between temperature and precipitation on continents over the range of latitude. Mean precipitation values from Hauschield *et al*., 1994.

of snowfields and possibly permanent ice. Beyond the mountains, the further depleted winds contributed to dry inland and western climates. In the north, westerly winds moving off the developing Indian seaway would have supplied some rainfall to the north-west. After the Aptian, the north apparently collected at least intermittent and local high rates of precipitation, suggesting that eastward-moving surface currents of the adjacent Tethys seaway represented a pool of easily evaporated warm surface waters, as is indicated by various Albian and younger climate indicators around the western and northern margins of the seaway (Chumakov, 1995).

Global sea-level remained low in the Early Cretaceous, but from the Valanginian (c. 141–135 Ma) a punctuated series of rises began that continued until the Turonian (c. 90–88 Ma). Short-term Early Cretaceous sea-level changes (on time scales of up to about 500 000 years) have been shown to correspond with oxygen isotope values, indicating that polar ice may have existed through this time (Stoll & Schrag, 1996). The extremely low sea-level of the Valanginian has never been repeated. In Australia, this history is reflected in the gradual encroachment of marine seaways in the west (Perth and Carnarvon Basins, and most extensively, the Canning Basin) and in the east-central region (Carpentaria, Laura, Surat and Eromanga Basins). The western seaways withdrew by the beginning of the Albian (c. 112 Ma), not to be seen again on the continent, while the Carpentaria/Eromanga seaway occupied as much as the central one-quarter of the continent throughout the Albian, but withdrew early

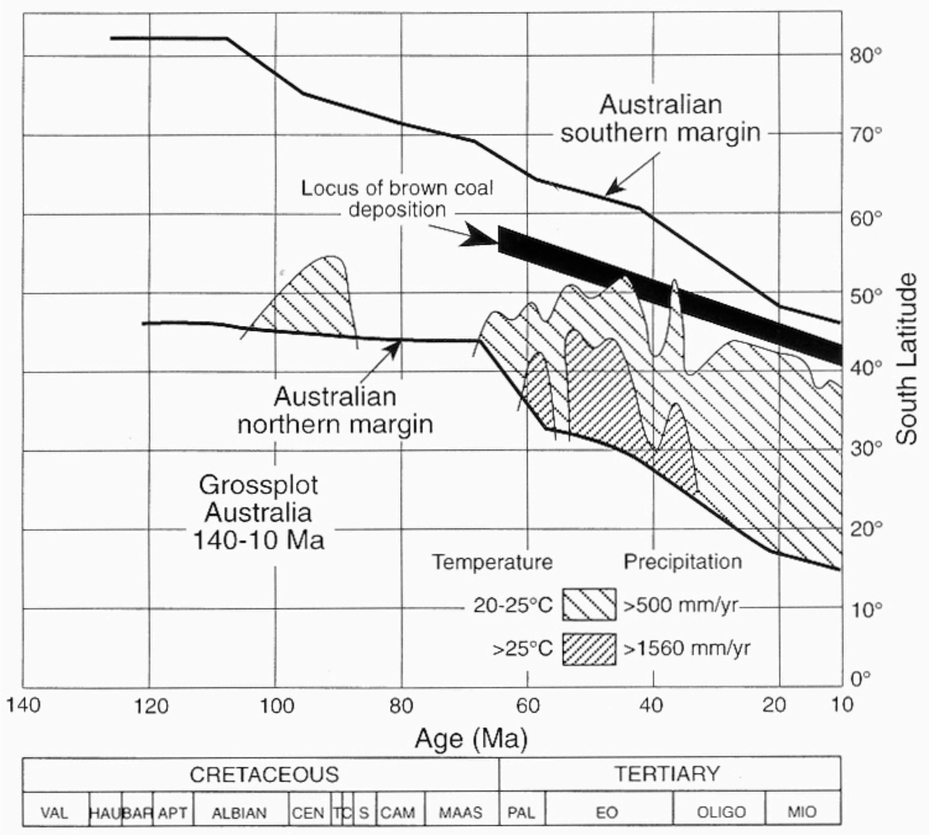

Figure 44. Space/time distribution of precipitation over Australia (<500, 500–1560, and >1560 mm/yr), Cretaceous to Middle Miocene, using the temperature/precipitation relationship of Fig. 43 and the distribution of palaeotemperatures from Fig. 41.

in the Cenomanian (c. 96 Ma; Frakes *et al.*, 1987). A major fresh water basin draining mainly to the north replaced the extensive Eromanga/Carpentaria seaway in the Cenomanian. The final major encroachment in the Cretaceous took place along the southern margin, beginning in the Late Albian in response to the opening of the Southern Ocean as Antarctica and Australia drifted apart. The opening of the Tasman Sea (Santonian to earliest Tertiary: c. 83–60 Ma) did not lead to development of new seaways on the Australian continent but initially permitted funnelling of cool high-latitude water northward along the present coast (Quilty, 1994). Late Cretaceous sedimentation was common, however, in the narrow Perth and Carnarvon Basins on the western continental margin, where periodic warm intervals are identified by the occurrence of specific foraminifera (Quilty, 1994). It is interesting that the sea-level record of Australia diverges most markedly from the global eustatic history (Haq *et al.*, 1987) precisely at the time of separation of most continental fragments from its margins, i.e. in the Late Albian. From then on, while global sea-level continued to rise for another 20 million years, the sea largely withdrew from Australia.

Tertiary evolution of climates towards the present

The climate history of Australia becomes much better documented from the opening of the Tertiary Period. The younger sedimentary materials are more abundant and generally more accessible than are older sediments. Furthermore, Tertiary fossil floras and faunas have closer relationships with their modern counterparts than do their ancestors and thus conclusions about their palaeo-ecological significance are more firmly based. Finally, marine climate indicators on the continent were more dispersed than previously, although the total area occupied by marine basins was only slightly larger than in the Late Cretaceous.

Evolution of the Australian climates in the Tertiary involved two significant factors. Firstly, the continent began a rapid transit to the lower latitudes, thus providing a background warming together with increased humidity, and secondly, the earth as a whole experienced progressive cooling, drying episodes. The balance of these opposed trends is reflected in slight warming over the Palaeocene to Mid-Miocene interval (c. 65–10 Ma) and more marked cooling since then. Throughout the Tertiary, fairly wide swings in temperature were apparent. Globally, the first indications of freezing conditions occur in the Middle Palaeocene, at which time ice rafting may have taken place in North Island, New Zealand (Leckie *et al.*, 1995). This event is interpreted as being probably short-lived, and the significant global cooling, as indicated by isotope records and Antarctic dropstones, began in the Middle Eocene (c. 55 Ma) (Frakes *et al.*, 1992).

Quantitative palaeotemperature determinations are not abundant for Australia in the Tertiary Period although there are abundant data which yield information of a qualitative sort, particularly for the Late Miocene and younger times. As indicated earlier, the climates of the Quaternary (the last c. 1.6 Ma) are not dealt with here, but information on modern climates can be found elsewhere in this volume (see Fox, this volume).

Palaeotemperatures during the Tertiary

Throughout the global record (Frakes *et al.*, 1994), and in Australia, the early part of the Tertiary Period presents a unique climatic picture, in this case characterised by evidence of very humid climates as well as high temperatures at middle to high latitudes. During this time, Australia moved northward at a rate exceeding 3 cm/y and into warmer climate zones. The south-eastern part of the continent remained at some significant elevation (Ollier, 1977).

Sources of information on the climates of this interval include several types of palaeobotanical/palynological investigations. Studies of foliar physiognomy of fossil plant materials have yielded quantitative palaeotemperature estimates for assemblages from South Australia, Victoria and New South Wales (Christophel, 1981; Greenwood, 1994). The most useful data of this type come from the Middle Eocene of southern Australia. Here, Anglesea (Victoria) yields a MAT range of 15–18°C, Maslin Bay (South Australia) a MAT range of

23–26°C, Garden Grove (South Australia) a range of 17–20°C, and Nerriga (New South Wales) a range of 16–21°C (Greenwood, 1994). On the basis of palynology and other fossil plant studies (Palaeocene to Early Eocene), the interior Lake Eyre region featured rainfall in excess of 1800 mm/yr and temperatures above 18°C (Sluiter, 1991). Fossil crocodilians, requiring year round temperatures of more than about 5°C, also are known from central Australia.

A recent study of Early Eocene foliar physiognomy and nearest living relatives (Greenwood & Wing, 1995) estimated southern Australian continental MAT as being between about 17°C and 21°C, and everywhere warmer than today. The paper presented the contrasts between data derived from such methods and the results of computer modelling of global climate, particularly as regards the continental interiors of Australia and North America. The latter efforts (e.g. Sloan, 1994) suggest sub-freezing winter temperatures (for the North American interior), greatly at odds with the palaeobotanical information derived from physiognomy and the environmental tolerances of nearest relatives such as palms. Climates of the Middle and Late Eocene (Langford *et al.*, 1995) may have been 2 to 4°C warmer than today, and rainfall in the extensive areas of *Nothofagus* rainforest may have exceeded 1500 mm/yr.

Carbonate sedimentation, indicative of bottom waters sufficiently warm that the minerals are not dissolved, but not necessarily documenting tropical temperatures, became a feature of southern Australia in the Middle to Late Eocene. Previously, carbonates had continued to accumulate on the North West Shelf (Apthorpe, 1988) and down the west coast to Cape Leeuwin at the south-western extremity, but now they were spread irregularly onto the southern marginal basins (Bremer, Eucla, St. Vincent, Murray and Otway Basins; Langford *et al.*, 1995). The initial stages of Great Barrier Reef development saw a wide area of carbonates accumulate on the Queensland Plateau at this time.

A major event in global climate history took place at the end of the Eocene (c. 35 Ma) (Frakes & Kemp, 1973). This was the marked cooling of the earth, which led to development of an ocean-atmosphere system similar to that of the present. This perhaps resulted from increased vigour in the lateral and vertical circulation in the world ocean, and marked expansion of the polar ice cap in Antarctica. The impact on Australia, still situated in relatively high latitudes, was immediate and of great significance for the environment, which had experienced warm, wet climates for most of the previous 25 million years For example, Kamp *et al.* (1990) recorded a drop in temperature from c. 20° to c. 13°C across the Eocene/Oligocene boundary, based on isotopic analyses on marine sites in southern Victoria. In addition, carbonates ceased to be developed on the Queensland Plateau in the Early Oligocene. Although the results are largely qualitative, palaeobotanical studies show marked changes in floras compatible with cooling (Macphail *et al.*, 1993, 1994). Perhaps predictably, due to the topographic relief, the south-east seems to have experienced continued high humidity.

The Oligocene to Middle Miocene world saw a slow and probably irregular warming, which is especially obvious in sea surface temperatures and calculated Antarctic ice volumes. From Deep Sea Drilling data, Zachos *et al.* (1993) suggest ice on Antarctica first reached its present volume in the Early Oligocene and may have attained 200% of the present volume at the Early/Late Oligocene boundary. Australian conditions mirror these trends (Feary *et al.*, 1991). Here, the effects included a return to carbonate sedimentation, of a temperate type, in the St. Vincent, Murray, Otway and Gippsland Basins, as well as renewal of carbonate deposition, and the first biogenic reefs, on the Queensland and Marion Plateaus. The Karumba Basin, located beneath the present Gulf of Carpentaria, likewise accumulated carbonates, and biogenic reef structures on the North West Shelf, which originated probably in the Middle Miocene, were common. Paradoxically, reefs did not develop in offshore Queensland waters during the Late Miocene and Pliocene, only recurring and continuing after the Pliocene. An explanation for these trends in sub-tropical waters can possibly be found in changes to circulation patterns in the low latitudes of the world ocean as a result of the changing thermal state.

The space/time diagrams for oceans and continents, contoured as to temperature (Figs 41 & 42), provide a means of estimating Australian palaeotemperatures for any time and palaeolatitude through the Tertiary until the end of the Middle Miocene. Remembering that the concept assumes that Australian temperatures conformed to the mean global values within latitude bands, it can be predicted that, with some notable reversals, particularly in low latitudes, Australian temperatures warmed more rapidly than the northward migration of the continent would suggest. If warming was due to migration alone, the isotherms should roughly parallel the orientation of the boundary. However, convergence of isotherms towards the southern (high latitude) boundary of the Australian time/space zone indicates a warming trend greater than that due to migration. Conversely, if there was a net cooling, isotherms would converge toward the northern boundary. The strongest warmings probably took place (in rank order) in the Middle Eocene, the Early Eocene and the Middle Oligocene. As for the coolings, the rank order would be the Early Palaeocene, Late Palaeocene-Early Eocene and the Late Eocene. To generalise, the Palaeocene-Eocene was a time of rapid change, while the Oligocene-Middle Miocene was characterised by more equability. Only the southern fringe of Australia appears to have endured MAT less than the present global MAT (c. 13°C) and this only during the interval from the Palaeocene to the Middle Oligocene. These quantitative estimates of temperature may be useful in deciding on the relative usefulness of fossil taxa in Australian palaeoclimatology.

Tertiary palaeotemperatures derived from space/time contours of the continents can also be compared with modern MAT on Australian palaeogeographic maps (Fig. 45). The important differences between Early and Late Tertiary climates immediately become apparent. Early Tertiary (Palaeocene and Eocene) climates are seen to be nearly everywhere cooler than at present. The exceptions are small coastal areas adjacent to the Tasman Sea and to sources of warm water from the equatorial zone, and there is a further area of warmth along the Victorian coast. But the Miocene maps show that over the entire continent, temperatures were likely to have been warmer than at present, a result perhaps not expected given the northward drift. The explanation lies in the fact that present temperatures reflect the general glacial condition of the Earth even though we are currently in an interglacial stage. The growth of polar ice which led to intense global cooling only began in earnest in the Late Miocene.

The estimates of Australian palaeotemperatures in Figs 41 and 42 collectively differ little from the geological data, thus suggesting that such plots can be used to supplement or expand on the 'hard' information. This compatibility also demonstrates that across Australia temperatures were not greatly different from those which characterised comparable global latitude belts.

Precipitation history

Indicators of precipitation or precipitation-evaporation balance in the past include the distribution of palaeosols by type, organic accumulations such as coals or peats and evaporitic deposits, in addition to information deriving from studies of plant materials themselves. Australia began the Tertiary in wet to extremely wet conditions, but a drying phase extending through most of the period was initiated in the Mid-Tertiary, probably during the Oligocene. According to Langford *et al.* (1995), evaporite formation in the Australian centre was a dominant process only in the Holocene, which suggests that extreme evaporative conditions did not characterise the region during the Tertiary.

Palaeosols are important, although qualitative, indicators of precipitation rates. Deeply weathered profiles containing abundant iron oxides and kaolinite clay minerals are considered diagnostic of seasonally high rates, while silcrete and calcrete profiles are more representative of drier, and in some cases alternating wet and dry, conditions. Many attempts have been made to date the episodes of weathering documented by abundant palaeosols in Australia. Taylor (1994) suggests that, taken together, these data show that deep weathering has been a long term feature during the whole of the Tertiary. Difficulties in determining the age of formation of fossil soils have led to a variety of dating methods being employed, the most recent utilising palaeomagnetism and the isotope geochemistry of clay minerals. Idnurm & Senior (1978) determined that fossil soils from several locations (south-western Queensland, southern South Australia, and near Perth, Western Australia) all possessed

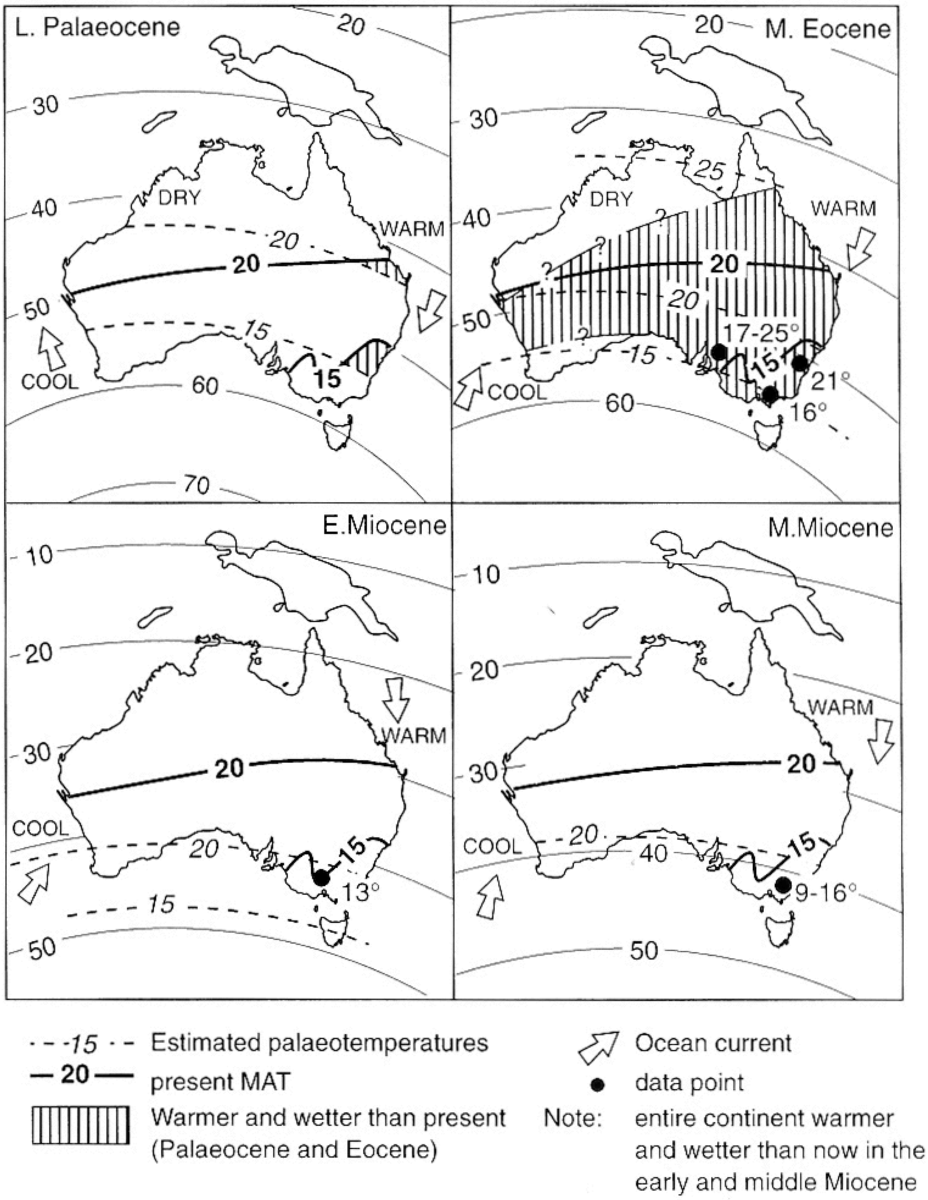
L. Palaeocene
20
30
40
50
60
70
DRY
WARM
COOL
20
15
M. Eocene
25
17-25°
21°
16°
E.Miocene
10
13°
M.Miocene
9-16°
- - -15 - - Estimated palaeotemperatures
— 20 — present MAT
Warmer and wetter than present (Palaeocene and Eocene)
Ocean current
● data point
Note: entire continent warmer and wetter than now in the early and middle Miocene

Figure 45. Palaeoclimatic elements of Australia during the Tertiary Period.

remnant magnetism consistent with formation during the Maastrichtian to Early Eocene (c. 74–50 Ma). Their study also suggested formation of another Queensland palaeosol in the Late Oligocene. McGowran (1979) accepted the Early Eocene as a time of deep weathering and high precipitation. He also suggested that the Late Eocene, the Middle Miocene and the Late Miocene experienced similar conditions, based on extra-tropical excursions of large foraminifera. Deep weathering to form major bauxite deposits requires an annual rainfall higher than about 1700 mm, less than 4 months of dry season and a MAT greater than 20°C (Tardy *et al.*, 1991). Australian bauxites are very poorly dated: 'Tertiary' is normally cited. Bauxites at Weipa, Gove, the Kimberleys and the deposits in the Darling Ranges were all located in the appropriate rainfall/temperature zone (Figs 44 & 45) during the Eocene, and thus would have conformed to the optimum conditions. Rainfall in the Perth region may have been insufficient for bauxites to form during the Miocene.

Other types of palaeosols can be used to interpret palaeoclimatic conditions. The most useful, calcrete or calcretised palaeosol, is considered to be the product of weathering in semi-arid environments where evaporation exceeds precipitation (Reeves, 1978). The great episode of pedogenic calcrete formation in Australia seems to have begun in the Mid-Tertiary and continues today. Silcrete is another guide to climatic humidity conditions, its development often being ascribed to arid settings, but because silcrete is frequently found as a component of lateritic soil profiles, it has also been suggested as an indicator of strongly seasonal climates (Stephens, 1978). A major episode of pedogenic silcrete formation around Lake Eyre, possibly related to silcretes extending north-eastwards over much of the Eromanga Basin, is dated as between Middle Eocene and Early Miocene (Alley *et al.*, 1996). A second Lake Eyre silcrete event is of Late Miocene to possibly Pleistocene age (Benbow *et al.*, 1995b). In central Queensland silcrete ranges may date back to the Late Miocene. To sum up, calcretes and silcretes support other evidence of increasing Late Tertiary dryness in the interior.

Brown coal, or lignite, is a common feature of the Australian Tertiary, ranging over sizeable areas of the south-east (Gippsland, Bass, Otway, Murray and St. Vincent Basins), in the Duntroon sub-basin and the Ceduna Terrace of offshore South Australia, and in association with deeply weathered profiles palaeomagnetically dated as Late Eocene in the Arunta Block of central Australia (Senior *et al.*, 1994). Long-ranging brown coal sequences (Palaeocene to Middle Miocene) developed in the Gippsland and Murray Basins. The deduced overall trends in precipitation through the Tertiary on the basis of such deposits are as follows.

- Palaeocene–Early Eocene: high rainfall especially in the south-east (Gippsland and Otway, but also in the St. Vincent and Eucla Basins, near Lake Eyre and along the north-west coast).
- Middle Eocene–Late Eocene: continued high humidity on the south coast (Gippsland, Bass and western part of the Nullarbor Plain) and in the centre (Arunta Block), as well as the north-west coastal area.
- Early Oligocene: a major drying out of the continent took place, with coaly deposits forming only in the Gippsland region and south-western New South Wales.
- Late Oligocene–Middle Miocene: despite the warming trend at this time, on the evidence of coaly deposits, only relatively small areas in the Gippsland and Murray Basins recorded high precipitation rates (Hocking *et al.*, 1976; Rogers *et al.*, 1995).
- Late Miocene–end Pliocene: continued relative dryness across the continent; no coals recorded.

In summary, the Tertiary record of coals suggests a decline in precipitation (or precipitation-evaporation balance) throughout the period.

Strong indications of Australian climatic conditions in the Tertiary come from climate-related studies on fossil plant and animal material. For the Late Oligocene to Middle Miocene interval, high rainfall is indicated by abundant lake deposits in the centre (Langford *et al.*, 1995), and rainforest conditions are suggested by the faunas at Riversleigh in north-central Queensland (Archer *et al.*, 1991). The Late Miocene saw a remarkable change due to widespread drying (Martin, 1977, 1991; Kemp, 1978; Sluiter & Kershaw, 1982; Truswell, 1993). The transition to the modern vegetation was largely completed by about 6.6 Ma through the widespread replacement of the abundant extant rainforest floras by xerophytic types. An example of the change to aridity can be seen in the reduction of *Nothofagus* as a component of fossil assemblages. Pliocene climates featured apparently short intervals of increased rainfall in southern Australia, and Bowler (1982) has suggested that, continent-wide, conditions first approximated those of the present by about 2.5 Ma (Late Pliocene).

It would be advantageous to summarise the information available from a wide variety of global sources into a quantitative precipitation chronology. This can be attempted by first using the contoured global temperatures (Fig. 41) to estimate the thermal condition on Tertiary Australia. Then, knowing the relationship between MAT and mean annual precipitation (Fig. 43), it is possible to suggest the distribution of rainfall over the continent through this period. Three bands are delimited:

1) less than 500 mm/yr, corresponding to temperatures less than 20°C;
2) 500–1560 mm/yr for temperatures in the range 20–25°C; and
3) greater than 1560 mm/yr for values above 25°C.

Figure 44 indicates that, assuming no unusual circumstances such as oceanic currents or upwelling and 'normal' continentality effects, northern Australia was very wet in the Palaeocene, the Eocene and the Early Oligocene. In the Eocene, very humid conditions extended almost halfway to the southern margin. Moderate rainfall prevailed over most of the continent and extended farther southward throughout the interval. The remainder of Australia, at the higher latitudes, appears to have been relatively dry. Figure 45 presents the information in a different way. It is apparent that the cooler-than-present continent in the Early Tertiary was also mostly drier (except in the south-east), while the warmer-than-present Miocene saw wet climates over a large proportion of Australia.

The usefulness of this method can be judged by a comparison of the foregoing trends with Australian data derived from geological indicators of precipitation. The Tertiary brown coals of the south, in South Australia and Victoria, lie adjacent to the belt of moderate rainfall, which establishes some reliability for this method of estimating precipitation from temperature. Lake Eyre fossil floras (Middle Eocene) lack significant proportions of *Nothofagus* and other indicators of high precipitation rates (Alley *et al.*, 1996). Further, the deeply weathered palaeosols described above lie within or near the zones delimited as very humid to moderately humid (Queensland, South Australia and Western Australia). Although only broad estimates can be obtained in this way, they are at least of a semi-quantitative nature, and may even prove to be of value in inferring tolerances of ancient plant taxa as regards rates of precipitation. Results derived by this method do not compare well with those of another study based on a conceptual model of climate, based in turn on the climate parameters governing the distribution of modern peats and evaporites (Parrish, *et al.*, 1982). The inferred rainfall patterns of the latter study show only occasional agreement with the location of Australian brown coals.

Summary

This account has outlined the temporal spacing of important continental and global events contributing to the history of Australian environments, and through these has examined the systematic interactions of landscape and climate over a long span of geological time. As in all such studies involving historical information, it is necessary to discriminate between the several types of evidence. The evidence of landscapes, as seen in global positioning of the continent, its relationships with other landmasses, and its orography, helps to sketch the framework in which recognised climates of the past have operated. The variation of climatic elements (derived from both global and, where possible, strictly Australian data) is influenced by features of the landmass, that is, by its palaeogeography in terms of altitude, continentality, and land-sea geometry. In a reverse sense, the intensity and type of climate exerts a control on landscape, primarily through erosional processes. While the causal mechanisms for well-defined climates of certain intervals at a regional scale can be confidently attributed to the influence of landscape on palaeoclimate (for example, the tectonic raising of mountainous terrain in south-eastern Australia in the Cretaceous; the likely high continentality effects of the Gondwanan Late Palaeozoic), the relative strengths of these continental versus global evolutionary factors in contributing to perceived palaeoclimates unfortunately remain uncertain. Here, we have applied global mean temperatures and precipitation rates of the past 140 Ma to the latitudes occupied by the continent and have introduced slight modifications to the perceived climates due to landscape. For earlier times, we lack adequate summaries of these climate parameters on both local and global scales, and thus neither the description of climates by latitude belts nor the reckoning of the landscape factors can be rigorous.

The primary control on the grand sweep of environmental evolution in Phanerozoic Australia has been the position of the continent on the surface of the Earth. The two lengthy periods when the landmass occupied the polar and sub-polar zones coincided with a time of severe global cooling, in the Late Palaeozoic, and another time of regionally intensive cooling, in the Early Cretaceous. These intervals can be considered as benchmarks in a broad cyclicity of climate and the cooling effects are seen in strata around the globe. Glaciation affected Australia from about 330 to 269 Ma, and ice rafting continued until about 250 Ma. Over much of this time, Australia was positioned in a manner very similar to that of Antarctica at present (c. 60–90° latitude), yet the only substantial ice sheet was limited to the elevated eastern part of the continent, and this could perhaps be attributed to the likelihood that significant moisture sources were limited to adjacent parts of the Pacific. It would appear that polar/subpolar climates were less cold than in the present interglacial stage and may have had MAT as much as 5° warmer than now, possibly in the range -2 to -30°C. The spread of Late Palaeozoic glacial deposits in many basins over a large proportion of Australia leaves open the possibility that ice sheets were more extensive than is now commonly thought.

The Early Cretaceous cooling, featuring ice rafting only, was more regional in scope and less intense; it lasted from about 140 to 110 Ma. Palaeolatitudes of the continent for this interval appear to have been about 40° to 70°, and MAT ranged from possibly as low as zero to as much as 15°C. These temperatures were significantly higher than during the height of Pleistocene glacial times, and would be from 5° to 12°C warmer than at comparable latitudes today (10° to -12°C). The driving force for seasonal ice development was the tectonic elevation of south-eastern Australia at a time when it again occupied the higher latitudes. In the Early Cretaceous, moisture sources to build ice were not as limiting as in the Late Palaeozoic because of the seasonal nature of the climate, and the southern Pacific was nearby.

Australia was probably in its warmest stages in the early part of the Phanerozoic (Cambrian Period). The time was also notable for widespread aridity, which in fact extended through the Early Palaeozoic until the Devonian. Low latitude positioning in the pathways of Cambrian trade winds moving along the join with Antarctica generated no appreciable precipitation, as most moisture would have been dropped in the New Zealand sector. Desiccated areas formed in the east and north. The trade winds eventually reversed to move towards the Queensland sector from Tasmania in the Silurian as the continent rotated. All geological evidence supports the idea of low latitude warmth and low precipitation and/or high evaporation rates from the Cambrian through to the later part of the Devonian, when the long drift into high latitudes began.

For the period between the two cool intervals (most of the Mesozoic Era), the climates of the continent remain largely hypothetical, with a shortage of information from climate indicators, particularly for the Triassic and Jurassic. Using a geochemical model to quantify consumption of atmospheric carbon dioxide during weathering of surface silicate rocks, Berner (1994) found that in the Early Mesozoic carbon dioxide was nearly at its lowest for the Phanerozoic. This suggests a type of reverse greenhouse cooling for the interval. Suggestions of at least regionally high rates of precipitation come from the sparse distribution of coal deposits and from the development of major riverine systems in the interior in the Early Mesozoic.

Finally, the slow warming of Australia since the Early Cretaceous is documented both from geological data and from estimates of global latitudinal controls on temperature and humidity. This resulted from the drift towards lower latitudes, and despite the progressive cooling of climates on a global scale.

Acknowledgments

I am greatly indebted to a large number of colleagues, who specialise in the area of geological history, for countless discussions, not to say arguments, about the often conflicting evidence for the past environments of Australia. Their contributions to this chapter began many years ago and continue to this day. Obviously, the workers are too numerous to mention without unintentional omission, a possibility I prefer to avoid by acknowledging them collectively. Such a course also absolves any colleague from any inaccuracy which might surface here.

My appreciation goes to Ms Sherry Proferes for finalising the figures from rather scrappy bits of paper, and to Mr Murray Rogers for unravelling some of the mysteries of the computer software.

Part of this work was supported by grants from the ARGS/ARC.

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PRESENT ENVIRONMENTAL INFLUENCES ON THE AUSTRALIAN FLORA

Marilyn D. Fox[1]

The nature of the flora of Australia can be fully appreciated only with a knowledge of the environment of which it forms a part. The contemporary Australian environment is in turn the product of past events that have moulded the special character of the continent (Frakes, this volume). This chapter canvasses features of the contemporary Australian environment: the physical factors that influence it and the biotic and historical factors that make it what it is today.

Portrait of a continent

To a large degree the environment of Australia is a product of where it is, how old it is, how big it is, its shape and relief. Added to this, and of greater significance to the biota, is the fact that it is isolated from other large land masses and is surrounded by extensive oceans.

Location

Much of the physical environment of a piece of land or ocean is predicated on its location. Australia's isolation, in terms of its oceanic environs, has great biotic impact, its geographical location (latitude and longitude) is of interest for the climate it receives, and its placement towards the centre of a large crustal plate conveys tectonic stability.

Southern Hemisphere: Oceanic Hemisphere

Australia is one of only two of the world's continents to lie wholly in the Southern Hemisphere. The other one, Antarctica, is ice-locked and does not support significant terrestrial vegetation nor significant permanent human occupation. The Southern Hemisphere contains two thirds of the world's oceans and Australia is located between the Indian and Pacific Oceans, with the Southern Ocean to its south. These vast expanses of water and their circulation patterns strongly influenced the Australian environment. At the Tropic of Capricorn, the fetch across the Indian Ocean is 67 degrees of longitude, from Vangaindrano in Madagascar to near Cape Farquhar in Western Australia (c. 4800 km), while across the Pacific is 140 degrees of longitude from Rockhampton in Queensland to Antofagasta in Chile (c. 14 000 km). To the south the Antarctic Adelie coast is 25 degrees south (c. 2800 km) of South East Cape in Tasmania. To the north of Australia are New Guinea and the shallow seas and island archipelagos that lead to south-east Asia.

This degree of isolation has contributed to the nature of the Australian biota, with relatively few immigrants from long-distance dispersal. The principal avenue of ingress to the continent is across the tropical archipelagos to the north of Australia. However, Australia has only been in close conjunction to these links to Asia relatively recently in geological time. The degree of mixing of the floras is notably low. Some Australian groups including *Ptilotis* (Amaranthaceae) (Stewart & Barlow, 1976) have dispersed into Sundaland (Indonesia), *Eucalyptus* has extended to Malesia and the Philippines (Chippendale, 1988) and a few grass genera have reached south-east Asia (Clifford & Simon 1981). Extremely few groups have been successful in extending their range much further. Some tropical plant groups have moved into northern Australia and their diluting influence has reduced the level of endemicity in the tropical flora: 14% endemic genera in the tropical zone compared with 46.6% in the temperate zone (Burbidge, 1960), a pattern repeated in the flora of Western

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Australia with 14% endemic in the Kimberley tropical flora compared to 75% endemic species in the South-West flora (Hopper *et al.*, 1996).

Meridional position

Australia extends from about 11°S (Cape York, Queensland, 10°41'21"S) to about 44°S (South East Cape, Tasmania, 43°38'40"S), and so is partly within the tropics and partly within the temperate zone. All of Antarctica lies south of the Antarctic Circle (67°S). The other two southern continents, Africa and South America, straddle the equator and have land linkages to northern continents. As such they have equatorial lands, and, in the case of South America, also extend much further south to 55°S and peri-polar conditions.

Both Africa and South America were more extensively glaciated during the Pleistocene ice-ages. With the retreat of the glaciers at the close of each ice-age, the land was colonised quickly by annuals, particularly by those of Laurasian origin. Partly as a result of this, and partly because of their longer connections to Laurasian continents, each of those continents has a larger representation of Northern Hemisphere plants. For example, the flora of central Chile has a high similarity to that of southern California because of their shared annuals (Kalin de Arroyo *et al.*, 1994). The absence of the reinvasions that occurred elsewhere, with the scouring and rejuvenation of soils accompanying the glacial retreats, and the land bridges to facilitate invasion, has helped to retain the high level of endemism in the Australian flora.

Australia is in the Eastern Hemisphere, and extends from c. 113°E (Steep Point, Shark Bay, Western Australia, 113°09'18"E) to 153°E (Cape Byron, northern New South Wales, 153°38'14"E). At the Tropic of Capricorn Australia spans approximately 35 degrees of longitude whereas the other southern continents span 25 degrees (South America) and 20 degrees (Africa). Australia is as a result a rather broad continent, 40° wide and 33° deep. The other southern continents are much more attenuated at their southern limits. In part, its breadth contributes to the continent's climate, as large global circulation patterns move roughly from west to east across the continent.

Position on Indo-Australian Plate

Australia is part of the Indo-Australian crustal plate. This huge segment of the Earth's crust includes the Indian subcontinent in its far north-western sector, much of the Indian Ocean, and all of Australia and the Tasman Sea. Australia occupies the centre of the plate and this has contributed to the tectonic stability of the continent. It is well away from the active edges which run through New Zealand to the east and through New Guinea to the north. The edges of the plates are zones of friction and have concomitant volcanic activity and mountain-building forces. As a result of its location Australia is the only continent with no active volcano. It did however have active volcanoes up until the end of the Tertiary and the basaltic flows from these coincide with the present day occurrence of much of Australia's rainforests (Beadle, 1981a). More recent volcanic activity (c. 8000 years ago) gave rise to the basalt plains of western Victoria, an area covered with grasslands until the early 1800s.

The absence of much recent volcanism affects the soils of Australia. Without the rejuvenation of glacial advances and retreats or the pedogenesis that results from volcanism, the Australian soils are extremely old and, as a result of the weathering and leaching over time, are generally low in plant nutrients.

Insularity

Antarctica and Australia also share the character of insularity (that is, they have no land linkages to other continents). This contemporary pattern is at odds with the configuration of the continents at earlier stages of the Earth's history. In the mid-Cretaceous some 100 Ma, Australia and Antarctica were joined, together with Africa, Arabia (including parts of Turkey and Iran), India, Madagascar, South America, New Zealand, New Caledonia and New Guinea (White, 1986; Frakes, this volume), and fragments of south-east Asia including most of Indonesia (Michaux, 1991). This massive continent is referred to as Gondwana (Suess in

Vickers-Rich & Rich, 1993), named after the Gond kingdoms. The Gond were the caretakers of sites in India at which important plant fossils (ancient seed ferns such as *Glossopteris*) were found in Carboniferous-Permian coal measures. Glossopterids provided some of the evidence for the supercontinent's reconstruction (White, 1986; Hill *et al.*, this volume). Plate tectonics caused the shearing of parts of the Earth's crust and the slow separation of the present-day continents and islands.

It is notable that Australia and Antarctica were the last remnants of Gondwana to separate, a long process that began possibly 100 million years ago between southern Western Australia (Hopper *et al.*, 1996), and certainly had proceeded across much of southern Australia by 53 Ma but which was only complete with the separation of Tasmania possibly some fifteen million years later. This long interval of time straddled the Cretaceous Period through to the Eocene, and saw the demise of the dinosaurs, the dominance of the conifers and the emergence of the first broad-leaved plant groups such as the great southern dicotyledonous families Proteaceae and Myrtaceae and the monocotyledonous Restionaceae (Johnson & Briggs, 1981).

Being an insular continent has implications for both the Australian biota and the natural environment. The long period of insularity has been a time of northwards rafting which has contributed to the unique nature of the assemblage of taxa within the biota. That same period saw shifts in climate, both globally and regionally with latitudinal migration, and they too have impacted on the biota and moulded its special features (Frakes, this volume). One plant group which has diversified under the changing environment is the Myrtaceous genus *Eucalyptus* and its close relatives. Fossils attributed to eucalypts have been found in both South America and New Zealand (Hill, 1994a). In each region the group apparently went extinct, but it flourished and diversified in Australia to have an estimated 800 species today (Mummery & Hardy, 1994).

The degree of isolation has varied over the past two million years. The Quaternary glaciations represent periods of time when the outline of 'Australia' expanded and the current large islands of Tasmania and New Guinea and many smaller coastal islands were all linked by land bridges to the continent. The term 'Australasia' is used in biogeography to delimit those lands which have, in geologically recent time, been linked to Australia. It does not include New Zealand, New Caledonia and other reasonably proximate islands, which have a much older separation from it.

The creation of these land bridges, lasting as long as the glacial period, allowed them to be colonised by terrestrial plants and animals from both sides. As a result there was mingling of floras that had been separate. With the onset of each interglacial, sea levels rose and the separate islands were recreated. These periods of isolation, lasting as long as the shorter interglacials, were vicariance events that, in some cases, led to genetic change and speciation.

Age

The third major factor that moulds the Australian environment is the great age of the continent. Parts of the continent are extraordinarily old. Indeed, the oldest known land surfaces anywhere on the globe are found in parts of Western Australia. Exposed portions of Precambrian shield (600 Ma–400 Ma) (Bird & Chivas, 1988) strongly influence the western two thirds of the continent. Elsewhere in the world Precambrian features have been buried under more recent deposition, while here in Australia they remain exposed at the surface. Some of the oldest fossils found anywhere in the world occur in the Pilbara region of Western Australia. These are 3.5 billion year old fossilised stromatolites (Playford, 1979). The major effect stemming from this great age is weathering, which has left a deflated topography (Fig. 49) and ancient leached soils.

Being a great distance from the active edges of a plate dictates an unusual tectonic stability. Age and stability both contribute to the nature of the soils. There have been few glacial advances and retreats or mountain building phases to rejuvenate soils, and as a consequence of weathering the soils are often impoverished.

Size

With a continental area of 7.7 million square kilometres, Australia is the smallest continent and represents 5.2% of the Earth's land. Although described by some as an island, it is ten times bigger than the next largest island in the Southern Hemisphere, Papua New Guinea (792 500 km^2). It spans over 3600 km north to south, 3190 km from Cape York to South Point, with a further 500 km to the tip of Tasmania. It is somewhat broader, extending c. 4000 km from east to west (Beckman, 1996). As an island continent, Australia has a very extensive coastline: 35 877 km (mainland) and a total of 59 736 km including all islands (AUSLIG, 1998).

Shape and physiognomy

That Australia is a broad rather compact shape, with an extensive 'interior' marks it for aridity. Australia is broadest at the subtropical region in the Southern Hemisphere, with a large part of the continent within the zone of influence of the dry global high pressure cells which circulate from west to east.

There are few mountainous regions in the west of the continent, so moist air from the Indian Ocean flows over a hot flat continent. This deflated landscape was the product of massive glacial erosion from 330–200 Ma (Hopper *et al.*, 1996; Frakes, this volume) and subsequent weathering with wind and water erosion. There has been little subsequent mountain building. The continent has an average elevation of only 330 m (Table 7), with plateaus, tablelands and rolling hills dominating the landscape. There are few long interior rivers, but many short coastal ones, particularly flowing from the Great Dividing Range in the east. The great salt lakes of South Australia and Western Australia are a striking feature of the arid centre of the continent.

There are few mountains and no great mountainous chains such as the Andes of South America. At 2745 m, Mawson Peak on Big Ben (Heard Island) is the highest point on Australian Territory. The lowest point is Lake Eyre at -15 m. The longest and most influential topographic feature in Australia is the Great Dividing Range in the east, which includes the tallest mountain on continental Australia, Mount Kosciuszko, at over 2200 metres. Each of the other continents has peaks with heights well over double that. The next lowest, Antarctica, with an average elevation of 2200 m (Table 7), has the Vinson Massif at almost 5140 metres (Allen, 1996). To the north and east of Australia are islands close to the tectonic plate's margins with much more impressive mountain chains. Puncak Jaya (Jaya Peak) in Irian Jaya is 5029 m, Mount Wilhelm in New Guinea is 4509 m and Mount Cook in

Table 7. Dimensions of the continents.
(Based on table 3.1, Jennings & Mabbutt, 1986).

	Australia	Europe	Antarctica	South America	North America	Africa	Eurasia
Area (× 10^6 km^2)	7.7	10	13.1	18	24.2	29.8	54.2
Area including continental shelf	11	10.8	15	20	31	31	65
Mean altitude (m)	330	290	2200	650	780	660	860
Highest point (m)	2228	5633	5140	6959	6193	5895	8848
Lowlands below 200 m (%)	39	57	6	38	30	10	25
Plateaus etc above 1000 m (%)	2	7	86	13	27	23	30

New Zealand is 3754 m (Allen, 1996). Only 13.2% of the land area of the Australian continent is higher than 500 m elevation, with only 0.01% over 2000 m (AUSLIG, 1998). With such a small part of the continent that can be described as alpine, there is as a consequence only a small alpine flora. However, it is of great scientific significance, and shares many genera with the Northern Hemisphere alpine flora (Barlow, 1989).

Climate

The Australian climate is strongly influenced by its high insolation (the amount of solar radiation reaching the surface), one outcome of the high pressure belts (anticyclones) which track across the continent. This strong radiation load causes high evaporation and, especially in arid central Australia, limits the growth of plants. Rainfall is highest in the east and north but there is marked seasonal differentiation between north and south. The northern parts of the continent receive intense summer rainfall from tropical depressions or monsoons. In the south, winter depressions bring rain to the southern portions of the continent. Between these two seasonal rainfall zones, the arid zone receives little rainfall, and this is aseasonal. In the south-east the summer and winter rainfall patterns overlap and this is the region of the continent with the best development of eucalypt forests. Beyond these broad rainfall patterns, the outstanding feature of Australia's climate is its variability. This variability is as great as for any other continent, and for some large regions such as the arid zone, may exceed that for comparable regions elsewhere (Fox, 1995).

Circulation Patterns

Oceanic circulation

Two significant oceanic currents influence the near-shore environment of Australia. These are the cold West Australian current, which swings from the southern Indian Ocean north along the western Australian coast in the summer. There is also a warm offshore current that flows south along the west coast of Australia, the Leeuwin Current (Pearce & Walker, 1991). This low-salinity, nutrient-deficient water prevents upwelling of cold nutrient-rich water, as happens on the west coasts of South and North America, Africa and Europe (Hopper *et al*., 1996). The Leeuwin current causes the winter rainfall of south-western Western Australia, as the warm near-coastal waters bring moisture that condenses over the cold land surface. The other significant oceanic current is the warm East Australian current which brings warm water south along the east coast of the continent. In part, these currents account for the existence of the extensive coral reefs in north-eastern Australia and their somewhat poorer development in the north-west of the continent. Nevertheless, tropical marine conditions extend further south on the west coast of Australia than anywhere else on Earth.

Atmospheric circulation

Australia occupies the same broad latitudinal band (c. 10°–43°S) through which swing the immense global mid-latitudinal high pressure cells, and this contributes to the continent being extensively arid. These anticyclones bring descending dry air to the broad areas of land through which they migrate in an eastwards direction. As the band shifts north and south seasonally with the Earth's precession, its total influence extends over fifty degrees of latitude, the full latitudinal extent of the continent.

The large anticyclones track across southern Australia at an average speed of 800 km per day and an average periodicity of 6.9 days (Specht & Specht, 1995). The centres pass to the south of the continent in summer but cross the continent in winter (Fig. 46). Within the Southern Hemisphere, the other land masses to intercept these anticyclones are parts of South America and Africa. However, neither of these are as strongly influenced by the high pressure cells as is Australia. This is mainly because there is a greater expanse of land exposed to them in

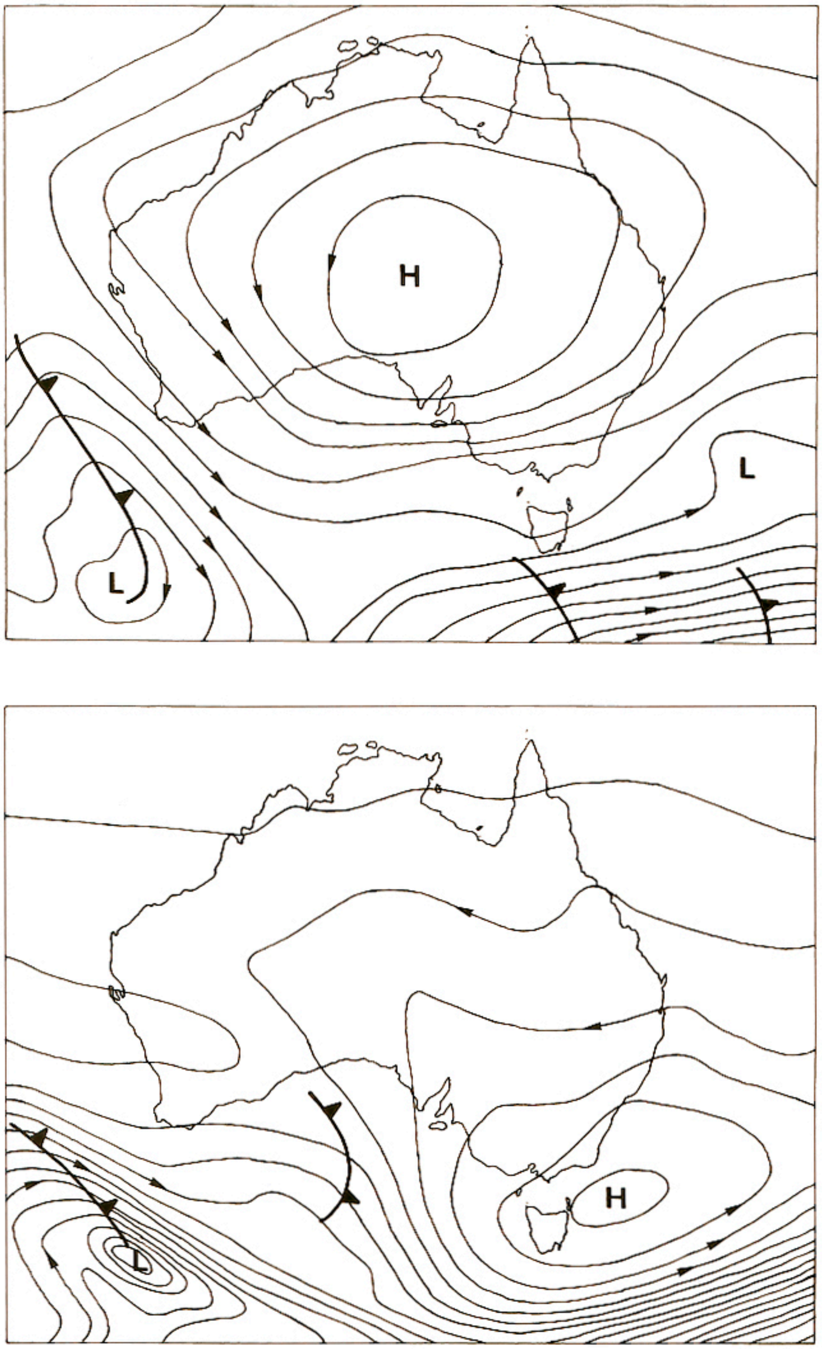

Figure 46. Typical Winter (top) and Summer (bottom) weather patterns. H = high pressure cell, L = low pressure cell, arrows indicate wind circulation directions. Drawn by P.McCarthy.

Australia. At 30° latitude Australia spans approximately 40° longitude whereas South America spans 22° longitude and Africa spans only 15° longitude. In addition, Australia is relatively flat and there is no strong rain barrier to intercept rainfall. In South America for example, the orographic effect of the long north-south barrier of the Andes running for over 7500 km somewhat nullifies the effect of the anticyclones. The vast continental 'fetch' of Australia contributes to its status as one of the driest continents.

Also contributing to northern Australia's unique climate is the large mountainous island to its north. Although one third of Australia is in the Tropics, New Guinea acts as an orographic barrier to tropical circulation of rain-bearing air. The great east-west trending mountains intercept moist tropical air, forcing it to high elevations where it cools and condenses, dumping high rainfall on the highlands of New Guinea. Dry air flows to northern Australia, which consequently is drier than it would be in the absence of this rain barrier.

Australia has a predominantly low elevation, particularly in the western half of the continent. The winds swing around high pressure cells in a counter-clockwise direction and so the prevailing winds over southern Australia are from the south-east although the weather patterns track from west to east. In the south-west there are some low ranges, such as the Darling Scarp and the Stirling Range, which intercept some rain-bearing moist air. From the south-west, air circulates over the extensive flat shield. Weather systems meet no more mountain barriers until the Flinders Ranges in South Australia and the Petermann and McDonnell Ranges in the centre. By then the air is warm and dry and little precipitation results.

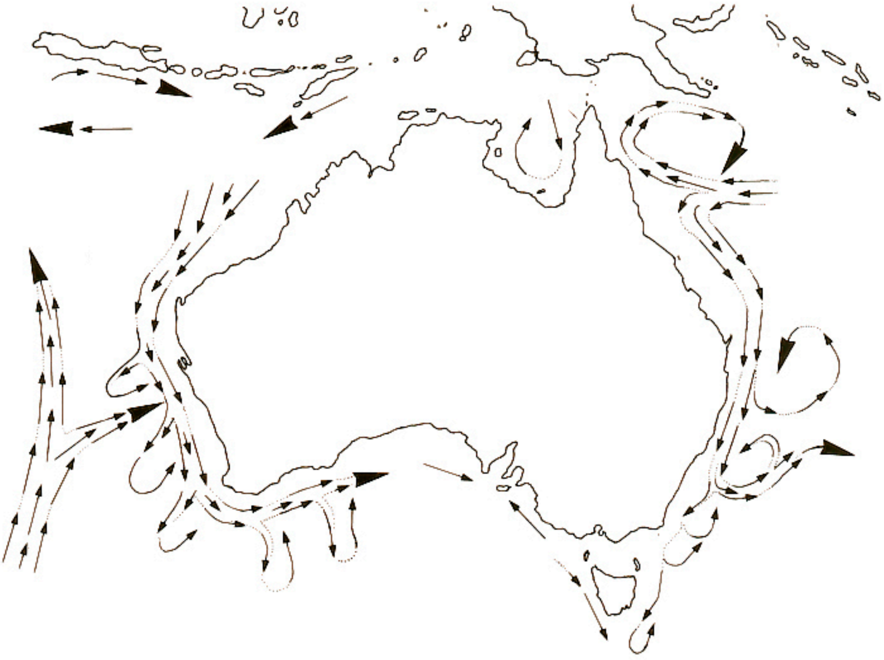

Figure 47. Ocean currents surrounding Australia. Source: Dr G.Cresswell, CSIRO Marine Research. Redrawn by P.McCarthy.

In the east is the major Australian mountain system, the Great Escarpment. To its west there is little orographic rainfall because of the long passage over the continental landmass. In the south, depressions may be deflected inland and bring rainfall to the eastern and south-eastern flanks of the ranges. When circulating winds bring moist air in from the sea to the south-east, rainfall can be intense. In the far north, tropical monsoonal depressions may cross the north-western coast or sections of the north coast, or extend further eastwards off-shore and then sweep south and westward to the east coast. Summer is the cyclone season and rainfall accompanying them is heavy. Tropical cyclones mainly occur between the latitudes 10°S and 25°S but have reached as far south as 30°S (Colls & Whitaker, 1990). This leads to some coastal regions having the highest annual rainfall records in Australia.

Tasmania differs markedly to mainland Australia. Much of the island's mountains are clustered in its western half, bringing high rainfall to the west, particularly the south-west, and the rainshadow depressing rainfall in the north-east.

Rainfall patterns and seasonality

Precipitation

Australia is the driest of the world's permanently inhabited continents (Table 8). Most of the precipitation is rain, with little snow and sleet. It also has the lowest percentage of rainfall as run-off, the lowest amount of runoff, the least amount of water in rivers and the smallest area of permanent wetlands (Dixon *et al.*, 1996). As well as these coarse temporal and spatial patterns of rainfall distribution, there are short-term patterns of rainfall intensity that affect the biological usefulness of the rain.

Australia has the lowest effective precipitation of any continent, because of variable and low precipitation and high evapotranspiration for much of the continent's interior. Evaporation is extremely high over much of Australia because of the generally high temperatures, low humidity and high insolation. In central Australia evaporation is many times greater than annual rainfall (Colls & Whitaker, 1990). For example, average annual evaporation is greater than 4000 mm in central Western Australia where the average annual rainfall is less than 200 mm. There are however parts of Australia where evaporation is much lower and rainfall is available almost year-round for plant growth. For western Tasmania average annual evaporation is less than 800 mm while average annual rainfall exceeds 1200 mm. As a result the area is extensively forested. For the continental margins, especially the relatively mountainous east coast, short rivers discharge much of the rainfall to the ocean. The result of these processes is an extensively arid landmass with less than a third of the area receiving sufficiently high and reliable rainfall to support woodlands and forests.

The long-term mean spatially averaged annual rainfall for Australia is c. 470 mm, but varies from year to year, being as high as 795 mm (1973) and as low as 370 mm (1965) in recent decades (Commonwealth of Australia, 1997). The rainfall is distributed unevenly across the continent, from the lowest average annual rainfall of 103 mm for Mulka in northern South Australia to 8352 mm at the summit of Mt Bellenden Ker south of Cairns in Queensland (Colls & Whitaker, 1990). The arid centre has extreme to very highly variable annual rainfall while only northern Australia, the southern edges of the continent and western Tasmania exhibit low variability.

The main belt of reliable rainfall is in the southern winter-rainfall parts of Western Australia, South Australia, Victoria and Tasmania, corresponding to the wheat belts of south-western and south-eastern Australia. This reliable rainfall also extends through parts of southern New South Wales.

In the north the summer monsoons from November to March are also highly reliable. The remainder of the year has a pronounced drought and the two strong seasons are known colloquially as 'the wet' and 'the dry'. The biota must survive these alternating wet and dry seasons, and the tropical woodlands of northern Australia contain facultatively deciduous species of eucalypt (*E. grandifolia*). Tropical grasses such as *Sorghum* spp. are vigorous annuals that grow rapidly in the hot wet summers; when they dry off in the winter dry season they provide abundant fuel for lightning and human-induced fire.

Table 8. Average annual water balance of the world. The seven continents ranked in decreasing order of effective precipitation (precipitation minus evaporation) or runoff. Estimated continental precipitation, evaporation, and effective precipitation are listed (Baumgartner & Reichel, 1975) and runoff figures* are from Brown (1983).

		Volume of water (× 10^3 km^3)			
Continent	Area (× 10^6 km^2)	Precipitation	Evaporation	Effective Precipitation	Runoff*
Asia	44.2	30.7	18.5	12.2	13.0
South America	18	28.0	16.9	11.1	16.7
North America	24.2	15.6	9.7	5.9	6.9
Africa	29.8	20.7	17.3	3.4	7.9
Europe	10	6.6	3.8	2.8	2.5
Australia	7.7	7.1	4.7	2.4	0.4
Antarctica	13.1	2.4	0.4	2.0	2.8
Land Areas		111	71	40	
Oceans		385	425	-40	
World		496	496	0	

Seasonality

Australia is highly influenced by the seasonal movement of the high pressure cells which bring seasonal drought to the north (winter) and the south (summer) of the continent. Rainfall pattern is the complement of these seasonal droughts: winter rain in the south, summer rain in the north, and a region of aseasonal or uniform rain in the south-east. In the southern winter the high pressure cells move northwards, bringing the rain-bearing depressions of the Southern Ocean into contact with the south of the continent. This leads to a zone of winter rainfall, in part mimicking the Mediterranean-type climate of summer drought and winter rain. At the same time the high pressure cells confer drought on northern Australia. Conversely, in the southern summer the high pressure cells have migrated southwards and northern Australia is exposed to the tropical low pressure systems and their monsoonal and cyclonic rains. In northern Australia the wet season (November–April) may account for over 90% of the annual precipitation; the dry season (May–October) may exhibit little to no rainfall. For example, Darwin receives on average 1453 mm in the 'wet' and only 83 mm in the 'dry' (from data in Colls & Whitaker, 1990).

This broad latitudinal pattern, northern summer rain with winter drought (north of 25°S), southern winter rain with summer drought (south of 35°S), is separated for two thirds of the continent by the arid zone (<250 mm per annum). This zone extends to the western coast of the continent. Rainfall in the arid zone is highly variable and may result either from southern trajectories of the tropical low pressure cells, or from southern winter depressions that occasionally extend further inland.

The eastern third of the continent, and particularly the narrow band east of the Great Dividing Range, may receive rainfall from either of these seasonal influences. Particularly for south-eastern Australia there is generally reliable rainfall throughout the year. This is the region with the greatest development of temperate forests, the most species of *Eucalyptus* and the greatest species diversity of birds (Saunders *et al*., 1996).

The energy budget

Insolation

Another consequence of inhabiting the latitudinal zone of the travelling high pressure cells are the clear skies for which Australia is famous. Without cloud-forming conditions, insolation is extremely high. Bright sunshine, averaged over the year, is greater than nine hours per day for all of the semi-arid and arid zones, and greater than six hours per day for all of the continent with the exception of western Tasmania (from fig. 2.13 in Colls & Whitaker, 1990).

The Bowen ratio is calculated as the ratio of the sensible heat flux from ground to air as a proportion of the product of the latent heat of vaporisation and the actual evaporation. The value for Australia is 2.18, much higher than the value for Africa (1.61) and Asia (1.14) (Gentilli, 1986). The ratio indicates that in Australia's high insolation environment more than twice as much heat is available to heat the air as is used in evaporating moisture. Nevertheless, as already discussed evaporation is however extremely high over much of Australia.

Temperature

As a result of the radiation load and conversion of much of this energy to sensible heat, day-time temperatures are very high, higher than equivalent latitudes elsewhere. For example tropical Australia is particularly hot compared to equivalent tropical regions elsewhere. The record this century was in January 1939 when it was 45°C in Sydney and 53°C in Cloncurry (northern Queensland) (Colls & Whitaker, 1990). Without extensive alpine areas, at Australia's latitudes, winter temperatures are not extremely low. The coldest recorded temperature was at Charlotte Pass not far from Mount Kosciuszko, which measured -23°C in June 1994 (Commonwealth of Australia, 1997). Temperature is, as a result, rarely limiting to plant growth. However, there are altitudinal zonations in plant communities that relate to minimum temperatures.

Variability and links to biota

El Niño Southern Oscillation (ENSO)

In addition to the mid-latitudinal high pressure cells, another significant global circulation pattern strongly influences the climate of much of Australia. This is the Walker Circulation (Commonwealth of Australia, 1997), in which warm air from the western Pacific rises and flows eastward in the upper troposphere to the eastern Pacific. There the air cools and descends, creating a high pressure zone off South America before the cooler air flows back westward across the Pacific. In some years this pattern is disrupted and the central and eastern Pacific Ocean warms and warm air rises (low pressure zone) where normally high pressures would prevail. This disruption in atmospheric circulation is driven in part by oceanic circulation, which results in upwelling of nutrient rich warm waters along the west coast of South America. As this happens in some years close to Christmas it has been referred to as El Niño, the 'boy child', the name coined in Peru. The intervening periods have been termed La Niña, times when the southern depressions are particularly active, resulting in very wet winters in the south of Australia (Commonwealth of Australia, 1997).

El Niño Southern Oscillation (ENSO), the term applied to this combined atmospheric and oceanic perturbation, clearly has a major influence on Australian climate. The impact on eastern Australia is drought in El Niño years. In recent decades there have been ENSO related droughts in 1972–73, 1982–83, 1987–88, 1991–92, 1994, and 1997–98. The region most affected is the eastern two thirds of Australia, part of the largest area of the globe most consistently affected by ENSO. This contributes to the overall variability in the Australian climate.

The ENSO-influence is also important in southern Africa, India, and parts of the Americas but not in Europe. Major Australian droughts coincide with ENSO events and extensive wet periods coincide with anti-ENSO events, which are somewhat predictable. ENSO-related droughts and wet periods have time scales of about one year, they exhibit very large (continental) spatial scales, they tend to be phase-locked with the annual cycle, and they are often followed/preceded by the opposite rainfall anomaly (Nicholls, 1991). This variability is expressed in the demographic patterns of the vegetation: 'the vegetation appears adapted to the climate in such a way that demographic composition is in a state of unstable equilibrium' (Nicholls, 1991: 31).

Bioclimatic interactions

Climate interacts with vegetation not as an amorphous influence, but as a series of limiting factors acting upon individual plants of each constituent species. Minimum temperature in the coldest month will limit survival of individuals of species requiring tropical or sub-tropical conditions, as will duration and degree of low humidity periods. Amount and timing of rainfall will influence which seeds can germinate and survive to maturity. Maximum day temperatures and duration of warm weather will determine whether particular species will be able to ripen fruits. Climatic factors also influence distribution of pollinators. All of these factors, and others more related to soils, fire frequency, etc, determine whether a species will be able to colonise or maintain itself within a particular area. Summation of these limiting factors over many species leads to the development of vegetation communities.

Recognition of these factors has led to the development of tools for predicting distributions of individual taxa, using known climatic parameters. BIOCLIM (Nix, 1982; Busby, 1991) is a particularly effective tool for bioclimatic matching. BIOCLIM is a form of geographic information system (GIS) with modelling capabilities. Climatic and geographic information for a 1.5 minute grid of the continent is recorded. The known distribution of a taxon can be plotted, and by climatic matching a predicted range can be generated. One application of the model is to record the known distribution of a taxon from fossil evidence and from this predict climatic parameters for previous periods (Busby 1986; Kershaw & Nix, 1988; Kershaw, 1997).

Nix (1982) had earlier introduced the classification megatherm, mesotherm and microtherm to define biogeographical regions based largely on thermal response. In this scheme, he employed a growth index that incorporated plant growth response to light, thermal and moisture regimes, but which is largely based on the temperature at which seasonal shoot growth is initiated. Megatherm (>25°C) biota resides in equatorial and tropical regions, Mesotherm (15–25°C) in the temperate zone and in equatorial and tropical uplands, and Microtherm (10–15°C), the cool temperate and alpine areas. These growth rhythms correlate reasonable well with the accepted components of the flora, indicating that they have been retained through a considerable time and through environmental change including climate change (Barlow, 1981).

Landforms and soils

Landforms

This most ancient continent has a subdued topography of plateaus, rolling hills and stony deserts with no active mountain ranges and relatively few plains. The major crustal subdivisions of the continent (cratons) are blocks of Pre-Cambrian shield and the more recent Tasman geosyncline. Together the blocks and interspersed basins create the structural elements of the physical landscape. These can be classified or grouped together as landform provinces or structural divisions or drainage divisions.

Jennings & Mabbutt (1986) divided the physiographic regions of Australia into three Divisions with twenty two Provinces. The three Divisions are the Eastern Uplands, the Interior Lowlands and the Western Plateau Division. Barlow (1986) has also proposed a series of regional landscapes which have been used in some publications of the Australian Biological Resources Study (Bridgewater, 1987). A more recent development is the description of a series of 80 terrestrial Interim Biogeographic Regions (IBRA regions, Thackway & Cresswell, 1995) which are also available on the ERIN WWW site. These are not landscape units *per se*, but were developed primarily to describe the state of the biota and to identify gaps in the national system of protected areas. However, by defining areas of principal ecosystems they naturally capture landscape units. They are, however, still under development, and to focus more on the landscape the classification by Jennings & Mabbutt (1986) is followed here, with cross references to the Barlow (1986) landscape region names interspersed.

Eastern Uplands Division

The Eastern Uplands are younger than the western part of the continent, more complex, with elevated remnants of the Tasman Fold Belt exposed in places. These uplands slope gradually westward to the Interior Lowlands and more sharply eastward to the narrow coastal plain. They comprise eight Physiographic Provinces (Jennings & Mabbutt, 1986):

- Great Barrier Reef Province: at 2,300 km this is the largest coral reef system in the world.
- Peninsular Uplands Province (Cape York; Barlow, 1986): the eastern half of Cape York, with various ranges, plateaus and tablelands, it has varied geology including some volcanic features such as the basaltic plateau of the Atherton Tableland. The climate is tropical and the vegetation comprises shrublands of *Melaleuca* and eucalypt woodlands on poorer soils, with rainforests generally on the richer soils (Bridgewater, 1987). Species-rich mangrove forests extend upriver from major estuaries.
- Burdekin Uplands Province (Burdekin; Barlow, 1986): north-eastern Queensland, primarily hills and lowlands, including the Townsville lowland which features the 'dry' tropics with anomalous low rainfall. Eucalypt woodlands occur in the ranges and lowlands, with rainforest where rainfall is highest (Bridgewater, 1987).
- Fitzroy Uplands Province (Dawson; Barlow, 1986): central eastern Queensland with predominantly sedimentary hills, plains and lowlands. A variety of woodlands clothe the varied landscape: *Eucalyptus crebra* woodlands on the ranges, *Acacia harpophylla* woodlands on the clay plains and *Allocasuarina* woodlands on the sandridges (Bridgewater, 1987).
- New England-Moreton Uplands Province (McPherson; Barlow, 1986): the central portion of the east coast straddling the New South Wales–Queensland border, various ranges, including the Border Ranges, and lowlands. The combination of basaltic soils and high rainfall allow for the development of subtropical rainforests at lower elevations and cool-temperate rainforest dominated by *Nothofagus* at higher elevations (Bridgewater, 1987). The tablelands and western slopes support open eucalypt forests.
- Macquarie Uplands Province (Nepean; Barlow, 1986): a varied province including the volcanic Warrumbungles, the Hunter Valley and the sandstone landscapes of the Hawkesbury–Shoalhaven Plateaus. A variety of eucalypt forests occur throughout this landscape, their species composition depending on elevation and substrate. Towards the coast a complex of coastal lakes, sandy plains and drowned river valleys such as the Hawkesbury, provide a variety of habitats including extensive mangroves and mudflats (Bridgewater, 1987).
- Kosciuskan [sic] Uplands Province (Howe; Barlow, 1986): which includes the Monaro Tableland (basalt and granite) and the volcanic Victorian Plains and Uplands. This province includes the Australian Alps and at high elevations there are alpine herbfields. The slopes carry a variety of eucalypt forests and the region extends to coastal bays and estuaries, some of which support Australia's best developed salt marshes (Bridgewater, 1987).

- Tasmanian Uplands Province (Tasmania; Barlow, 1986) which includes the Bass Strait islands as well as Tasmania. Tasmania has a distinctive array of vegetation types, including extensive cool temperate rainforest dominated by *Nothofagus*, wet plains dominated by *Gymnoschoenus* (buttongrass), alpine areas, and tall eucalypt forests (Bridgewater, 1987).

Interior Lowlands Division

The Interior Lowlands are mostly arid and semiarid with flat, low lying and generally deeply weathered Mesozoic and Cainozoic sediments. These occupy central eastern Australia and comprise vast flood plains and low-relief landforms. This division coincides with the Great Artesian Basin which is an ancient feature of the continent's interior drainage 1–2 million years old (Torgersen *et al.*, 1991). The principal river system, the Murray-Darling River Basin, forms the major part of the Interior Lowlands. The Murray-Darling is the continent's largest drainage basin. It drains one seventh of the continent, and ranks with the world's biggest rivers is terms of length (2520 km) and catchment area, but has a relatively very low annual discharge. All of the continent's largest lakes are salt lakes, normally dry, and form part of the major internal drainage system in the Interior Lowlands: Lake Eyre (South Australia) 9475 km^2, Lake Torrens (South Australia) 5745 km^2, and Lake Gairdner (South Australia) 4351 km^2. Lake Eyre has filled only three times this century.

Jennings & Mabbutt (1986) recognised three physiographic Provinces within this Division:

- Carpentaria Lowlands Province (Carpentaria; Barlow, 1986): the western half of Cape York and the Gulf of Carpentaria lowlands. A range of vegetation types include tropical grasslands (*Dichanthium* or *Astrebla*), *Melaleuca* shrublands, *Acacia* and eucalypt woodlands, rainforest scrub, and mangroves (Bridgewater, 1987).
- Central Lowlands Province (Thompson, Cooper, Warrego and Simpson; Barlow, 1986): a huge area including the floodplains of the Diamantina, Cooper, Bulloo and Paroo Rivers, the Simpson Desert dunefield, Sturt Desert plains, the Eyre–Frome plains and the major salt lakes of South Australia. The principal vegetation types are the *Astrebla* grasslands of the plains, with *Triodia* grasslands dominating in the more arid portions. Sandy soils support *Callitris* woodlands, while clay soils have *Acacia harpophylla* in the east, *A. aneura* in the west, or *Allocasuarina lepidophloia* woodland (Bridgewater, 1987).
- Murray Lowlands Province (Darling and Riverina; Barlow, 1986): the plains of western New South Wales and western Victoria, including the Riverine Plain and Wimmera Plain. Riparian forest of tall *Eucalyptus camaldulensis* grades to woodlands on the clay plains, which may be dominated by *Eucalyptus largiflorens* or by *Acacia* species. Rocky ranges have *Callitris* and eucalypt woodlands, while dunefields support mallee communities. The heavier soils of the riverine plains are vegetated with a chenopod shrubland which may be dominated by species of *Atriplex* or *Maireana* depending on topography (Bridgewater, 1987; Fox, 1991).

Western Plateau Division

The massive and ancient Western Plateau comprises the main Archaean and Proterozoic structural elements, now dominated by sand plains and low tablelands with emergent ranges (MacDonnell, Hamersley, Stirling, Flinders Ranges). The central and western Australian ancient plateaus are more than 100 million years old and the stony or sandy deserts are of great antiquity. This plateau is extensively arid, except in the south-west and far north. For two long sections of coastline, for about 1500 km of the Western Australian coastline from Carnarvon to south of Broome, and at the head of the Great Australian Bight between Esperance and Ceduna, the arid zone extends to the coast. Australia's major deserts are in the Western Plateau Division: the Great Victoria Desert (Western Australia and South Australia) 348 750 km^2, Great Sandy Desert (Western Australia) 267 250 km^2, Tanami Desert (Western Australia, Northern Territory) 184 500 km^2, and the Gibson Desert (Western Australia) 156 000 km^2, while the Simpson Desert (Northern Territory, Queensland, South Australia)

176 500 km^2, is in the Interior Lowlands Division (AUSLIG, 1997). Unlike extensive deserts on other continents, these support perennial vegetation in the form of hummock grasslands (*Triodia* and *Plectrachne*) and groves or scattered trees of a number of genera including *Acacia*, *Allocasuarina*, *Eucalyptus*, *Grevillea* and *Callitris*.

Comprising two-thirds of the continent, the Western Plateau Division is divided into twelve Provinces (Jennings & Mabbutt, 1986):

- North Australian Plateau Province (Arnhem; Barlow, 1986): principal features are dissected plateaus, including the Arnhem Plateau, and alluvial plains. Open-forest comprising various eucalypt subgenera is the dominant vegetation type (Bridgewater, 1987). This grades to woodland in the interior. Sandy soils support a heathland which shares a number of genera with heathlands found in temperate regions.

- Kimberley Province (Kimberley; Barlow, 1986): includes a variety of geological features, such as the Kimberley Plateau, Fitzroy Plains and Ranges. Vegetation ranges from dry rainforest to grasslands in the south. Extensive stands of mangrove and saltflat vegetation occur in the tidal estuaries (Bridgewater, 1987).

- Carpentaria Fall Province (Carpentaria; Barlow, 1986): the western half of the Gulf of Carpentaria and the Isa Ridges. Grasslands dominated by species of *Astrebla* occur on clay soils, and *Melaleuca* shrublands on sandy soils (Bridgewater, 1987).

- Lander–Barkly Plains Province (Barkly; Barlow, 1986): comprises most of tropical Northern Territory south of the Arnhem Plateau, including dunefields and sandplains with dissected sandstone plateaus. The calcareous clay soils support grasslands dominated by *Astrebla* species and there are scattered woodlands in drainage lines (Bridgewater, 1987).

- Central Australian Ranges Province (Macdonnell; Barlow, 1986): southern Northern Territory, including the Macdonnell, Henbury, Petermann, Musgrave and Warburton Ranges. This complex province has a diversity of vegetation to match the diversity of landforms. There are hummock grasslands (*Triodia* spp.), *Acacia*, *Allocasuarina* and *Eucalyptus* woodlands, and shrublands with semi-succulent chenopod genera (*Atriplex* and *Maireana*). The deep gorges of the Macdonnell Ranges contain relictual taxa such as the palm *Livistona mariae* and the cycad *Macrozamia macdonnellii* (Bridgewater, 1987).

- Sandland province (Sandy Deserts, Gibson and Victoria Desert; Barlow, 1986): central Western Australia including the Great Sandy, Great Victoria and Gibson Desert dunefields. Primarily hummock grasslands (*Triodia* spp.) but in depressions and drainage lines there are woodlands and dense thickets of *Allocasuarina*, *Acacia*, *Callitris* and *Eucalyptus* (Bridgewater, 1987).

- Pilbara Province (Pilbara; Barlow, 1986): includes the Hamersley Plateaus and lowlands and hills of a range of geologies. Hummock grasslands of *Triodia* spp. are the most widespread vegetation type, with Mulga (*Acacia aneura* complex) woodland on the floodplains and scattered eucalypts on the rocky ridges (Bridgewater, 1987). As in most parts of the arid and semi-arid zones rivers and creeks are lined by River Red Gum (*Eucalyptus camaldulensis*) or by Coolabah (*E. microtheca*, syn. *E. coolabah*).

- Western Coastlands Province (Murchison, Bencubbin, Leeuwin and Esperance; Barlow, 1986): extends from the Onslow Plain to the Leeuwin Peninsula. This latitudinally extensive province includes a variety of vegetation types, from Mulga (*Acacia aneura* complex) shrublands, mallee and heathlands to the tall forests of *Eucalyptus diversicolor* (Karri).

- Yilgarn Plateau Province (Leonora; Barlow, 1986): extensive outcropping of Pre-Cambrian Shield, includes the goldfields of Western Australia. The principal vegetation is *Acacia aneura* woodlands grading to mallee in the south.

- Nullabor Plain Province (Nullabor; Barlow, 1986): principally the Bunda Plateau, a karst plain of limestone. Much of the region is covered with low chenopod shrubland with species of *Atriplex* and *Maireana*, with mallee along the coastal fringe (Bridgewater, 1987).

- Eyre Peninsula Province (Eyre; Barlow, 1986): includes the Gairdner Plain, dunefields and low hills. Mallee is the most extensive vegetation formation, although this has been cleared in much of the province for wheat farming. Extensive salt marsh and mangrove systems occur at the head of St Vincent and Spencer Gulfs (Bridgewater, 1987).
- Gulfs Ranges Province (parts of Eyre and Torrens; Barlow, 1986): Flinders and Lofty Ranges, Yorke Peninsula, with plains and tablelands. The rocky ranges carry eucalypt and *Callitris* woodlands while the plains are dominated by *Acacia* woodland and chenopod shrublands (Bridgewater, 1987).

Soils

The consequences of latitude and physiognomy would not necessarily dictate the present Australian environment if it did not also have its extreme antiquity. Because much of Australia is so old, the soils have experienced prolonged periods of weathering. As it has not experienced many orographic episodes neither has there been opportunity for replenishment. Australia was little influenced by the great Pleistocene glaciations, and so was not rejuvenated periodically as were extensive areas of the Northern Hemisphere in particular. The soils therefore are very old and leached, resulting in a low pool of available plant nutrients, particularly phosphorus and nitrogen, but also sulphur and potassium, and the trace elements molybdenum, copper, zinc, boron and manganese (Williams & Raupach, 1983).

These oligotrophic soils have influenced the nature of the Australian flora. The bulk of the flora is scleromorphic, but to what extent this relates to the aridity of the growing environment as opposed to the nutrient status of the soils they grow in, is still to be fully resolved. However, features evolved to cope with low nutrients may also have aided the plants in an increasingly fire-prone environment.

Principal soil types

There are no classes of soils unique to Australia (Lindsay, 1985). Some soils are more common here than on other continents, including unconsolidated sands, texture contrast soils and the cracking clays of regions such as the Hay Plain in New South Wales. Australian soils differ from those in the Northern Hemisphere in three main ways: they generally have lower organic matter content and poorer surface structure (Noble *et al.*, 1996) and have a preponderance of mycorrhizal fungi. The fungal symbionts of many native plants are essential for nutrient uptake and recycling in oligotrophic soils.

Northcote (1986) classified Australian soils into those that result from deep weathering or shallow weathering of parent material. More recently this classification was modified by Isbell (1996). The soils of the arid zone all result from deep weathering and are primarily red siliceous sands, earthy sands and earthy loams (rudosols and tenosols; Isbell, 1996), particularly in the Sandland Province of Western Australia. These and other 'earths' and 'ironstone gravelly duplex soils' (kandosols; Isbell, 1996) cover the ancient landscapes of the western and central portions of the continent. The deep weathering mostly occurred during the warm, wet conditions of the Tertiary, and as a result large areas of western and central Australia are covered by laterites. The lateritic caps are resistant to weathering and erode slowly, but underlying clays erode more rapidly leading to the formation of flat-topped mesas (Bridgewater, 1987).

Soil groups resulting from shallow weathering include the calcareous earths and cracking clays (vertosols; Isbell, 1996) of southern Australia which support the chenopod shrublands. Northern Australia has mainly shallow, often stony soils. Saline and sodic soils are common in Australia (44.9% of Australasia; Szaboles, 1979). Salinity is measured by the chloride ion content whereas sodicity is measured by exchangeable sodium ions. Sodosols have various nutrient and physical limitations to plant growth.

Links to flora and vegetation

Particularly depauperate soils in Australia frequently support some of the most spectacular assemblages of the flora. For example, calcareous sands form the sandplains north of Perth and support the extremely rich kwongan vegetation (Pate & Beard, 1984). This low shrubland is rich in members of the families Proteaceae, Myrtaceae, Fabaceae, Mimosaceae, Epacridaceae and Liliaceae. It supports the highest levels of alpha diversity (species richness) on the continent (Rice & Westoby, 1983). Similarly the skeletal sandstone soils of the Hawkesbury plateau, shallow and lacking structure as well as being oligotrophic, support much of the species-rich Sydney sandstone flora.

The soils of southern Australia (east and west) are generally considered to be the poorest in plant nutrients of all the 'Mediterranean' regions (Williams & Raupach, 1983). The eastern part of the 'Mediterranean' region of Australia is relatively more fertile than is the far south-west (Lamont, 1994). Eastern mallee communities commonly occur on aeolian calcareous brown earths, while in the west mallee communities grow on duplex soils with a distinct sandy and lateritic horizon over a clay horizon (Hill, 1989). There is a preponderance of calcareous soils in the eastern mallee and of non-calcareous soils in the west (Blackburn & Wright, 1989).

The understorey associated with mallee stands is dependent on rainfall and soil type. Fox (1994) recognised five types of understorey, combining work of Specht (1972), Beadle (1981a) and Fox (1990):

- on slightly more fertile, but saline, soils the understorey features halophytic shrubs of the families Chenopodiaceae and Zygophyllaceae. As these grade to more saline or more water-logged conditions mallee becomes absent and low halophytic shrublands predominate;
- on infertile soils with intermediate rainfall, a dense thicket of *Melaleuca* and/or (*Allo*)*Casuarina* forms the understorey. This is the 'mallee-broombush' of Specht (1972). In places mallee eucalypts overtop the thicket, but elsewhere the eucalypts may be missing. This is particularly well developed in the eastern mallee sector, in western Victoria and parts of South Australia;
- on infertile soils in wetter areas a rich shrub layer of xeromorphic shrubs (families Proteaceae and Myrtaceae) forms the understorey of what is referred to as 'mallee-heath' and which may be ecotonal. This occurs particularly nearer the southern coastal regions;
- on infertile soils in the driest areas, the understorey is of xerophytic, hummock grasses (*Triodia* spp. and *Plectrachne* spp.). As rainfall declines the mallee becomes progressively less frequent and is finally absent, and the hummock grasslands continue into the arid interior of the continent; and
- when mallee remains unburnt for a long time and much woody litter accumulates, the understorey may comprise only annuals. These now comprise both natives and introduced annuals, and in highly disturbed sites introduced species predominate.

Within a landscape unit there is large-scale vegetation patterning, and both structure and floristic composition of the mallee can vary on a topographic scale of tens of metres (Fox, 1990). In swales between dunes conditions may be quite saline and the chenopod understorey may predominate. On the flanks of the dunes the understorey is heathy, while on the crest it may be dominated by *Triodia*. Similarly, there are topographically related shifts in mallee species dominance, and the same catena from swale to dune crest may involve five or more eucalypts. Similar local shifts in mallee community composition have been recognised in the western region (Beard, 1990). At a broader landscape scale there is also topographic and edaphic control of mallee and other communities (Fox, 1991).

Hill (1989) recognised eight mallee biogeographical 'groups' (Table 9) on the basis of their floristic composition, but also taking into account habitat, including soil type. 'The mallee habit is apparently of different age in different groups and areas, but present-day occurrences are closely correlated with edaphic factors which in turn are dependent on rainfall, substrate, and land-form' (Hill, 1989: 95).

Table 9. Principal Australian mallee biogeographical groups: relationship between biogeographical region (W: south-western Western Australia, E: east of the Great Australian Bight), floristic composition (subgenera), number of mallee species, habitat including soil type, and associated vegetation. (Based on table 6.1, Hill, 1989).

	Subgenera	Number of mallee species	Habitat	Associated vegetation
1W	*Eudesmia* *Symphyomyrtus* *Monocalyptus*	5 60 9	Lateritic sandplain	'Kwongan' extremely rich
2W & E	*Eudesmia* *Symphyomyrtus* *Dumaria* *Monocalyptus*	3 14 8 5	Calcareous coastal dunes on Pleistocene and Holocene dunefields	Shrub thicket with *Eucalyptus, Banksia, Acacia* or *Melaleuca*
3W	*Symphyomyrtus* *Dumaria*	23 10	Mallee woodland	*Cratystylis, Melaleuca*, chenopod understorey
4W	*Symphyomyrtus* *Monocalyptus*	12 4	Siliceous dunes from granite and quartzite	Shrub thicket
5W & E	*Corymbia* *Eudesmia* *Symphyomyrtus*	2 4 31	Aeolian desert dunes	Hummock grassland understorey
6W & E	*Corymbia* *Blakella* *Eudesmia* *Symphyomyrtus* *Exsertaria*	3 1 2 11 8	Arid zone rocky ridges	Shrub savanna and hummock grass with *Acacia* in upper stratum
7E	*Symphyomyrtus*	6	Mallee boxes	Mixed shrubby with *Acacia*
8E	*Monocalyptus*	14	Mallee ashes, high rainfall	Low scleromorphic shrub understorey

The *Eucalyptus* subgenus *Symphyomyrtus* is clearly the dominant eucalypt group of mallee vegetation, particularly in the western region. Its constituent species are predominantly of mallee habit, with few obligate monopodial trees. By comparison, other subgenera comprise predominantly tree-forms with fewer mallee-forms. Facultative mallees are those species which can on more fertile or deeper soils produce trees, but when stressed produce the multi-stemmed mallee habit.

The richest mallee communities are located in south-western Western Australia. Hill (1989) has recorded up to 20 species in a few hectares near Ravensthorpe, the common range being 8–10 species (Beard, 1981). The mallees of south-eastern Australia are less rich, 3–4 sympatric eucalypt species being the norm (Fox, 1990a).

Vegetation

'Apparently, the vegetation of Australia is more original than its flora, and more original in some areas than in others.' (Doing, 1981: 7).

Special features of the flora and its relationship to the vegetation

Vegetation is the term used for the assemblages of plant species that have a particular structural characterisation. What is special about the Australian vegetation is the wealth of the flora that comprises it and the special nature of that flora. Estimates of the total flora range from 20 000 (Introduction to this volume) to 21–23 000 species of vascular plants (Mummery & Hardy, 1994). Of these, 85% occur here and nowhere else, that is they are endemic to Australia. There are 14 families of flowering plants that are endemic to Australia (Beadle, 1981b; Briggs in Mummery & Hardy, 1994), a figure exceptionally higher than that for any other continent (but note that not all of these are recognised as distinct families in *Flora of Australia*). It is also an exceptionally high proportion of the 56 families of plants that are endemic to any one particular region (Cox & Moore, 1985). The non-flowering plants are also well represented in Australia. For example, the pteridophyte flora consists of 111 genera (*Flora of Australia* Vol. 48, *Introduction*), about 40% of the world's total, the algal flora is estimated to contain 22 000 species (Saunders *et al*., 1996) and Australia has 2800 species of lichens (Filson, 1996).

Beadle (1981b) referred to three ancestral assemblages: the *Nothofagus* assemblage, the broad-leaved rainforest assemblage and the herbaceous cold-climate assemblage. The *Nothofagus* assemblage included the conifers and some angiosperm families such as Cunoniaceae, Epacridaceae, Winteraceae and others (Beadle, 1981b). This vegetation type extended across southern Australia and as far north as parts of northern Queensland, although at higher elevations. Its contraction during the Tertiary was from west to east, and there is fossil evidence from sites which today are semi-arid (Martin, 1973). This vegetation type may have persisted until the early Pleistocene in such locations. Today it is restricted to parts of Tasmania and isolated localities on the mainland.

The broad-leaved rainforest assemblage ('*Cinnamomum*' flora; Beadle, 1981b) was widely distributed across the continent in the Eocene and reached its maximum development in the Mid-Tertiary. This assemblage included members of the families Lauraceae, Moraceae, Myrtaceae, Proteaceae and others (Beadle, 1981b; Hill, 1994b; Hill *et al*., this volume). With the increases in aridity in the late Tertiary this forest type also contracted. Presumed rainforest relictual taxa such as the Leopardwood (*Flindersia maculosa*) of western New South Wales are remnants of this much more widespread vegetation type. Another significant outcome of this environmental change was the evolution of new genera from this flora with xeromorphic adaptations (Beadle, 1981b). These diversifications occurred extensively in the Myrtaceae, Proteaceae and Rutaceae.

Table 10. Examples of each of the floristic elements used by Barlow (1981) for the major plant formations used by Specht (1981c).

Formation	Pangean	Gondwanan	Autochthonous	Post-Miocene	Recent (<200 yr) Invasive
Closed forest	Kauri Pine *Agathis* sp.	*Gunnera* *Nothofagus* *Placospermum*	very few	*Agapetes* sp. *Rhododendron* sp.	*Thunbergia grandiflora*
Tall open forest	Tree ferns *Cyathea* spp.	*Banksia* spp.	*Eucalyptus* spp.	very few	*Cryptostegia grandiflora*
Open forest	Cycads *Macrozamia* spp.	*Dillwynia* spp.	*Eucalyptus* *Xanthorrhoea*	very few *Viola* sp.	*Lantana camara*
Woodland	Cycads *Lepidozamia* spp.	*Flindersia* sp.	*Acacia* spp.	very few	*Mimosa pigra*
Shrubland	Cypress Pine *Callitris* spp.	Trigger plants Stylidiaceae	*Leptospermum* spp.	very few	*Echium plantagineum*
Heathland	? Post-date Pangea	*Banksia* spp.	*Grevillea* spp.	very few	*Chrysanthemoides monilifera* *C. rotundata*
Grassland	Post-date Pangea	May post-date Gondwana			
- Hummock			*Triodia* spp.	very few	*Acacia nilotica*
- Tussock			*Astrebla* spp.	*Poa* spp.	*Prosopis spp.*

Beadle (1981b) also postulated an herbaceous cold-climate assemblage shared between Australia, New Zealand and South America. Remnants of this flora are extant in parts of southern Western Australia and South Australia and as annuals in the arid zone.

Beadle's three assemblages were based on fossil evidence of pre-existing vegetation types. Barlow (1981) emphasised two conponents in the contemporary flora, the relictual (Gondwanan) and the Australian (autochthonous) component. The relictual component contains extant taxa which had their origins in the *Nothofagus*, broad-leaved rainforest or herbaceous cold-climate assemblages. These are now mainly confined to moist habitats and exhibit taxonomic affinity to parts of the floras of similar habitats on other Gondwanan remnants (Barlow, 1981). The autochthonous component is derived from ancestral Gondwanan taxa which diversified in reponse to the changing environment. This component exhibits high levels of endemism and is characterised by scleromorphic characters which evolved in response to low nutrients and increasing aridity.

The different elements of the flora are not restricted to any particular vegetation type (Table 10), except perhaps in the case of the temperate rainforests. The species of the flora that coexist in particular vegetation types may have different lineages and even in communities noted for their autochthonous element, such as coastal heathlands, there may be much older members such as cycads which are possibly Pangaean in origin. Specht (1981a, 1981b) recognised 32 plant formations in Australia and studied the distribution of 1285 genera represented in them (Barlow, 1981). Specht concluded that almost every formation contained a mixture of genera from the different floristic elements.

Beadle (1981a) considered the endemic families and genera in relation to their habitat. Of the twelve families he considered, four are confined to rainforests and all of these are monospecific, the rest occurring mainly on soils of low fertility or in the arid zone (Table 11). These habitats have seen the greatest evolutionary changes, a pattern which is repeated at the generic and species level (Tables 11 and 12). Of the 538 endemic genera Beadle considered, a total of 301 (56%) were assigned to either the nutrient-poor, humid habitat or the arid habitat type. An additional 54 genera from the 'unclassified' group are found on these habitat types, making a total of 355 or 66% of all endemic genera. The preponderance of these uniquely Australian taxa within environments which have only become widespread since separation from Antarctica emphasises the role of environmental change as an evolutionary force.

Table 11. The endemic families and their broad habitat type. (Based on table 4.1, Beadle, 1981a). Two other endemic families are now recognised (Briggs, in Mummery & Hardy 1994). Note that not all of these families are recognised in Cronquist's system, as used by *Flora of Australia.*

	Rich soils, humid	Poor soils, humid	Range of habitat, generally poor soils	Total
	Family (gen./spp.)	Family (gen./spp.)	Family (gen./spp.)	Families (gen./spp.)
Dicotyledons	Austrobaileyaceae (1/1) Akaniaceae (1/1) Idiospermaceae (1/1)	Chloanthaceae (10/66) Tremandraceae (3/28) Baueraceae (1/3) Cephalotaceae (1/1) Eremosynaceae (1/1)	Gyrostemonaceae (5/15) Brunoniaceae (1/1)	10 (25/118)
Monocotyledons	Petermanniaceae (1/1)	Cartonemataceae (1/7)		2 (2/8)
Total Families (gen./spp.)	4 (4/4)	6 (17/106)	2 (6/16)	12 (27/126)

At any one time only a fraction of all the plant species that potentially occupy a site may be visible: the other species are present only as dormant seed in the soil seed reserve. This is particularly the case in the arid and semi-arid regions where rainfall is sporadic and unpredictable. For example, permanent 0.1 hectare sites in western New South Wales have recorded 90+ species of vascular plants over a decade of sampling, but at any one collection the number represented by mature plants may be as low as 17 and as high as 45 (Fox, 1988). Even in very good seasons, there are apparently mechanisms that limit the number of species co-occurring.

In Australia a few genera numerically dominate the composition and character of the vegetation. In particular the tree stratum of most open forests comprises eucalypt species (*Eucalyptus* and *Corymbia*). The eucalypts are now thought to number over 800 species (K. Hill *pers. comm.*) and are widely distributed. In many woodlands and shrublands members of the genus *Acacia* are dominant and influence the character of the vegetation. *Acacia* in Australia has about 950 species (Maslin, 1995) and dominates the vegetation of much of semi-arid and arid Australia but also can occur in rainforest and alpine areas. It is richest in Western Australia. The family Proteaceae is also particularly diverse in Australia. Of the c. 75 genera in this family, 46 occur in Australia and, of these, 37 are endemic. There is a total of c. 1100 species in the family in Australia (*Flora of Australia* Vol. 16). Members of the genus *Grevillea* rarely dominate the canopy of vegetation but they are a conspicuous component of coastal shrublands as well as semi-arid woodlands, again being most species-rich in Western Australia. Another family of note are Casuarinaceae. Members of the genera *Casuarina* and *Allocasuarina* are locally dominant in coastal communities as well as arid and semi-arid woodlands.

There are a number of other ways in which the Australian vegetation differs from that of other continents. There are very few deciduous tree species. One species of *Nothofagus* is winter deciduous and there are a few species of tropical eucalypts which are drought deciduous, the dry season also being winter. There are relatively few conifers and those that are present do not dominate whole vegetation types as is the case in the northern temperate regions, although *Callitris* can form local woodlands in semi-arid areas. In the arid zone there are no members of the Cactaceae or other large succulents (Moore & Perry, 1970).

Table 12. Number of endemic angiosperm genera (and families these represent) confined to specific habitats. (Based on table 4.2, Beadle, 1981a).

	Rich, humid	Poor, humid	Arid	Cold	Unclassified #	Total
Dicotyledons	76	136	94	17	90	413
Monocotyledons	10	58	13	2	42	125
Total genera	86	194	107	19	132	538
Total families	36	12+	31	11		92

# genera which extend over more than one habitat.

Structural classification of vegetation

The distinction of 'flora' or floristic composition versus 'vegetation' or structure has influenced the description of vegetation in Australia. Some authors such as Beadle (1981a) emphasised the patterns in distributions of key elements of the flora, while others such as Specht (1981c) used a classification based solely on structure. Doing (1981) presented a map of the phytogeographic regions of Australia based on a mixture of criteria of flora and vegetation. He distinguished two subkingdoms, the *Eucalyptus* subkingdom and the Central Australian subkingdom in which the dominant genus is *Acacia*. In many aspects the *Eucalyptus*/*Acacia* division of Bridgewater (1987) is close to this subdivision.

The description of vegetation in Australia has for a long time stressed the structural attributes of the vegetation. In 1960 Wood & Williams erected both a two-way classification scheme and an alphanumeric formula for referring to each 'form' of vegetation. The table had as the row entries, the life-forms from tree (>8 m) to herbs, and as the columns the 'density or coverage' of the dominants in four divisions: very dense, dense, mid-dense and open (Wood & Williams, 1960, table 8). Subforms of each vegetation form were distinguished by leaf texture, single or multi-stemmed and single or multistoried. This structural classification was

Table 13. Two-way classification of typical Australian plant communities. (Based on table 4.1, Specht, 1981c). The triplet notation (Beard & Webb, 1974) is code for the dominant genus*, life-form and foliage projective cover. The number of genera of vascular plants is given for some formations (Specht, 1981a), and for tall closed forest (Rainforest Conservation Society of Queensland, 1986).

Life-form	Foliage projective cover % (of upper stratum)			
	100–70% (4)	70–30% (3)	30–10% (2)	<10% (1)
Tall trees (T) (>30 m)	xT4 Tall closed forest, rainforest 516 genera	eT3 Tall open forest, eucalypt 157 genera	*not extensive in Australia*	*not extensive in Australia*
Medium trees (M) (10–30 m)	xM4 Closed forest, rainforest 70 genera	eM3 open forest, eucalypt 124 genera	eM2 woodland, eucalypt	eM1 open woodland, eucalypt
Low trees (L) (<10 m)	xL4 closed forest, rainforest	eL3 low open forest, eucalypt	eL2 low woodland, eucalypt	eL1 low open woodland, eucalypt
Tall shrubs (S) (>2 m)	mS4 closed scrub, *Melaleuca*	eS3 mallee open scrub, eucalypt	aS2 tall shrubland, *Acacia* 150 genera	aS1 tall open shrubland, *Acacia*
Low shrubs (Z) (<2 m)	xZ4 low closed shrublands	xZ3 heathlands 290 genera (SW), 236 (SE)	kZ2 low shrublands, chenopod	kZ1 low open shrublands, chenopod
Hummock grasses (H) (*Triodia* & *Plectrachne*)	*not extensive in Australia*	*not extensive in Australia*	tH2 hummock grasslands 88 genera	*not extensive in Australia*
Grasses/ graminoids (G)	y/gG4 closed tussock grasslands	y/gG3 tussock grasslands	aG2 grasslands *Astrebla*	sG1 open grasslands *Stipa*
Herbaceous plants (forbs) (F)	not extensive in Australia	not extensive in Australia	not extensive in Australia	xF1 open forb field

* For T, M, L : x = mixed dominant genera, e = *Eucalyptus*
*For S, Z : m = *Melaleuca*, E = *Eucalyptus*, a = *Acacia*, x = mixed, k = chenopod (*Atriplex* or *Maireana*)
*For H, G, F : t = *Triodia*, y = other grasses (e.g. *Danthonia s. lat.*), g = graminoids,
a = *Astrebla*, s = *Stipa (*now *Austrostipa)*, x = mixed.

later modified (Specht, 1981c) and is a very useful framework for the description of vegetation based on a few easily identified characters, the height of the dominant stratum and the foliage projective cover. It establishes a simple nomenclature for broad vegetation types devoid of colloquial terminology. This is also a classification scheme suited to continental vegetation mapping such as the natural vegetation of Australia (Carnahan, 1976; see also Figs 52, 53). A triplet formula was devised by Beard & Webb (1974) to capture both the structural attributes and to indicate the dominant genus. In most cases, at smaller scales, researchers modify the structural name with reference to the dominant species, so that greater floristic information is also captured. This is essentially the classification used by Groves (this volume), which should be consulted for a discussion of each element.

Floristic classification of vegetation

A different approach to classification of the Australian vegetation was taken by Bridgewater (1994). He classified the continent's vegation into 37 Divisions, 26 of which were based on floristic composition, and 11 on ecological factors. Each Division was described using both 'character genera' and notes on ecological and structural parameters. This classification is discussed in more detail, and mapped, in Groves (this volume).

Pattern related to climate

Phytogeographers and climatologists have attempted to calculate indices that may be useful predictors of vegetation structure based on climatic data alone. Prescott & Thomas (1949) devised an index based on the efficiency of rainfall in any month and which is calculated from both the precipitation and evaporation. The index is $P/E^{0.75}$ and using the number of months for which the value exceeds 0.4 (0.8 for vegetation with low transpiration rates) as the growing season they calculated that plants in the arid zone have on average less than one month, woodland less than five months, and sclerophyll forests greater than nine months of growing season.

Whittaker (1975) devised a simple schematic figure which distributed the world's biomes with respect to mean annual temperature (ordinate) and mean annual precipitation (abscissa). The triangular distribution produced ranges from tundra where both the mean annual temperature and mean annual precipitation are very low, to desert where temperature can range widely but average annual precipitation is less than 50 mm, to the other apex, where temperature and precipitation are high, and tropical rainforest results. An average climate for Australia has been calculated using BIOCLIM (Busby, 1991). The mean annual temperature is 21.5°C and the average annual rainfall is 451 mm (Bridgewater, 1987). Using these figures, 'Australia' falls in the semi-desert category of Whittaker's distribution of global biome types. Clearly the entire continent does not share this characterisation but it is an interesting observation.

The descriptions of the principal vegetation types of Specht (1981c; see Groves, this volume for a discussion) are arranged by the structure of the vegetation alone. These formations are distributed geographically with respect to climate, landforms and soil types. Bridgewater (1987) provided a continental vegetation map using floristic descriptors and listed the following map units for the three broad climatic regions: tropical/sub-tropical, semi-arid and temperate. Doing (1981) in his 'botanical geographical map of the Australian plant kingdom' had similarly considered the geographical distribution of vegetation as it related to climate. He had however, linked the tropical, subtropical and temperate vegetation within the same *Eucalyptus* subkingdom.

Tropical/Sub-tropical evergreen wooded vegetation

This is predominantly tropical eucalypt woodlands (Bridgewater (1987) distinguished the separate subgenera), some tropical and subtropical rainforest and mangrove forest. It extends from Broome across northern Australia to north of Townsville on Cape York. Tropical *Acacia* woodland occurs as far south as the New South Wales border.

Semi-arid grassland and shrublands

The most extensive vegetation communities in Australia are the *Triodia* grasslands of central Australia and the *Acacia aneura* shrublands to their south. Together they encompass most of the arid and semi-arid regions. To the east, particularly in south-western Queensland the Mitchell grass plains (*Astrebla* spp.) occupy the semi-arid region which has summer rainfall. Where winter rain predominates, and where the soil is naturally saline, chenopod shrublands (*Atriplex* spp., *Maireana* spp.) span southern Australia. On aeolian sandy soils, and where winter rainfall is over 400 mm but less than 700 mm per annum, multi-stemmed eucalypts form mallee communities. These have a discontinuous distribution across south-western Australia almost to the Head of the Great Australian Bight, and then occur extensively on Eyre and Yorke Peninsulas, Kangaroo Island, and from the mouth of the Murray through western Victoria and into south-western New South Wales.

Temperate forests, grasslands and shrubland

These separate almost exclusively into a set of communities only found in south-western Western Australia and a larger set found in south-eastern Australia and Tasmania. In both regions woodlands dominated by species of *Eucalyptus* subg. *Symphyomyrtus* with shrubby or grassy understoreys are the most extensive communities, and in both regions these have been extensively cleared for cropping. These communities occur in the better watered temperate regions of Australia, and except for very limited amounts of alpine shrubland and Buttongrass (*Gymnoschoenus*) sedgeland in Tasmania, *Stipa* grasslands of the basalt plains of Victoria, and the kwongan (Pate & Beard, 1984) shrublands of Western Australia, they are woodlands and forests.

As well as varying latitudinally, climate varies on an elevational gradient. In Australia elevational relief is very restricted but there are parts of the Southern Alps where there is a tree line at 1982 m at Mt Kosciuszko (36°27'S) and at 1676 m further south at Mt Buller in Victoria (Moore & Perry, 1970)

Fire

Fire is an integral part of the Australian environment. Possibly more than on any other continent, fire has played a pivotal role in shaping the biotic environment of Australia. The continent's isolated passage from Antarctica to its present location was coupled with a growing aridity of much of the continent. This fostered a fire-prone environment. The incidence of lightning strikes is high, especially in the semiarid and arid zones, and extensive late summer fires may result from them. There was no doubt an historical nexus between increasing aridity and increasing fire frequency resulting from lightning strikes, leading to the predominance of sclerophyll vegetation types today (Singh *et al*., 1981). The scleromorphic nature of much of the vegetation means that it has a high fibre, or fuel, content. That it also has a high concentration of flammable oils and terpenes adds to its flammability.

The arrival of Aboriginal and Torres Strait Island people accentuated an existing pattern of significant fire in the landscape. Aboriginal and Torres Strait Island people use fire as a tool to manage the landscapes they occupy. Evidence of this can be found in the charcoal records of sediments, the record of peaks of charcoal coinciding with the arrival of people in the landscape. Indeed, evidence of fire was often interpreted as evidence of occupancy in the eyes of the first European people to view Australia. All of the journals of early explorers note particularly the smoke they saw as evidence of people in the vicinity. In his journal James Cook (Beaglehole, 1968) noted fire many times, for example as his ship passed Cape Howe: 'In the afternoon we saw smook in several places by which we knew the country to be inhabited.' (Beaglehole, 1968: 287).

The much later arrival of significant numbers of European people and their different attitude to the use of fire signalled changes to the Australian landscape that are still being played out.

Role in the evolution of the flora

The flora has developed a number of traits which are useful in a fire-prone environment (Gill, 1975, 1981; Groves, this volume). In some species the adult plants can survive fires and renew growth after the fire by vegetative sprouts from lignotubers, epicormic buds, subterranean structures or from pre-existing meristems. Some plant communities feature a large proportion of species that are capable of resprouting in one of these ways. The oligotrophic and fire-prone heathlands of eastern Australia may have over 70% of their plant species capable of surviving fire (Fox & Fox, 1987). At the other extreme are species where adult plants cannot survive fire. These species must re-establish from seed, which may be held on the plant (serotony), in the soil seed reserve, or in some cases, depending on the period between fires, may disperse into the site from unburnt vegetation nearby. Post-fire succession comprises different combinations of these strategies, but for most sclerophyll communities the high proportion of vegetative resprouting species make it close to an 'initial floristic composition' with slight modification (Noble & Slatyer, 1980).

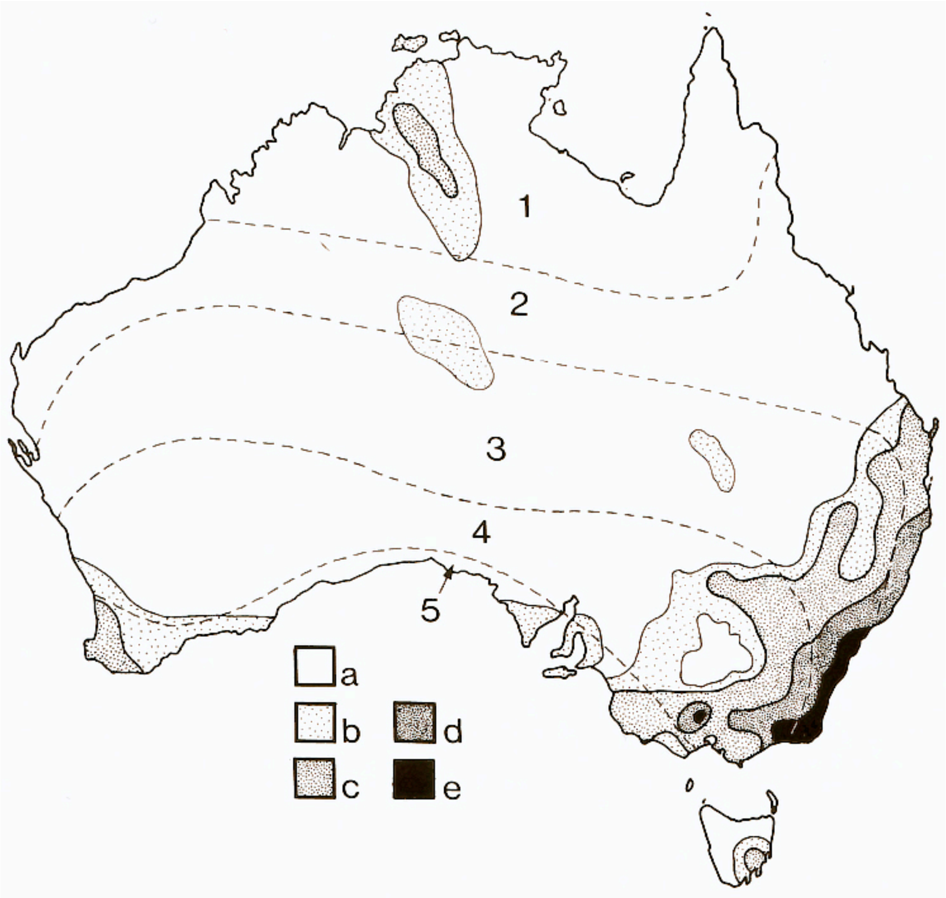

Figure 48. Frequency of bushfires. Occurrence of large bushfires: **a**: once in more than 10 years; **b**: once every 20 years; **c**: once every 10 years; **d**: once every 5 years; **e**: once every 3 years. Season: **1**: winter and spring; **2**: spring; **3**: spring and summer; **4**: summer; **5**: summer and autumn. Source: Redrawn (P.McCarthy) from AUSMAP Atlas of Australia, 1992. Original map copyright © Commonwealth of Australia, AUSLIG. All rights reserved.

A problem for the continued management of natural vegetation is maintaining a fire regime that is sympathetic to the fire-ecology of the species. In many inner urban parks, and national parks close to urban areas, fire management may be limited to frequent low-intensity fires, rather than the less-frequent, intense fires that may have been the natural regime. Indeed many inner urban areas are burnt regularly not by prescription but by arsonists. Such a regime will result in a different vegetation to what was there originally because it will discriminate against those species with slow maturation (Benson, 1985) and will promote the 'fire weeds', either native or introduced. The other extreme, protection from fire, leads to the loss of those species that require fire to rejuvenate their population base (M.Fox & B.Fox, 1986b). The absence of fire may lead to local extinction for such species just as swiftly as the frequent fire eliminates the slower maturing species.

People in the landscape

Arrival and impacts of Aboriginal people

At some time in the Pleistocene people entered northern Australia. The oldest dated human occupation is 50 000 years B.P. (Roberts *et al.*, 1990) but the suggestion, from rock engravings and from palynological sites, is that the date is much older. The general perception is that these people did not bring any other species of animals or plants with them, the introduction of the dingo being relatively recent. However, they did manipulate their biological environment with selective harvesting of edible plants, the cultivation of 'bush gardens', and the use of fire to drive game animals, to provide 'green pick' for game animals, to 'clean the country', and to maintain corridors.

By a combination of both habitat change and direct predation, Aboriginal people have been implicated in the demise of the megafauna (Merrilees, 1968; Flannery, 1994). The removal of large herbivores from the landscape would have impacted directly on the vegetation. The removal of large predators would also have implications for the population levels of their prey, mostly herbivorous animals, and this would in turn indirectly impact on the vegetation. However, the magnitude of these changes or the role of other environmental change is still the subject of much debate.

In these ways, the resident indigenous people had modified the Australian landscape before the arrival of other people. When European settlers arrived on the east coast it has been estimated that the Aboriginal population may have numbered 750 000 or higher (Butlin, 1983).

European settlement

The legacy of millennia of Aboriginal occupation, and Aboriginal fire management, was the landscape first viewed by European eyes. This was no doubt an altered landscape, different to what it may have been had the continent been untouched by humans. Indeed, the alarm signal fires of the indigenous people may have given the early explorers a distorted view of both the population size of the resident people, and the incidence of fire in their landscape (Kershaw, 1997). With the arrival of Northern Hemisphere colonists came a different attitude to fire, and the start of changes that are still occurring two centuries later (Benson & Redpath, 1997).

A fortunate aspect of the timing of the arrival of European settlers in eastern Australia was its coincidence with a blossoming of interest in natural history in Britain. For this reason the expedition of James Cook included two botanists and a botanical artist to record their discoveries. Indeed it was one of these, Joseph Banks, who was most influential in the establishment of the colony in Sydney and who is recognised in the generic name *Banksia*.

Unfortunately, another cultural development at the time of settlement was the rise of acclimatisation societies. Started in Britain in 1860, but already operating in France, these groups aimed to introduce and rapidly domesticate new food animals to Europe from the newly explored territories of Africa, Asia and the New World. These (still extant) societies also aimed to introduce 'innoxious' species to Australia. However, many were 'amenity' additions, such as the intentional introduction of house sparrows, blackberry, Indian myna, privet for hedges, etc. Such intentional introductions forced a more rapid naturalisation process than might naturally have occurred, and led to a new mix of species with introductions from distant lands.

Vegetation clearance

European settlement brought other unprecedented changes, paramount being the large-scale clearing of vegetation. The landscape today, particularly in the south, is a patchwork of remnant habitat often interspersed in large swathes of alienated land.

With the spread of settlement, land was cleared preferentially, the more fertile or more easily cleared communities going first, with concomitant loss of vegetation. The result after two centuries is a halving of the forest estate, with some vegetation types extirpated (Benson, 1991). For example, 85% of Victoria's box-ironbark forests and woodlands have been cleared, with remnants of this community now only found on upper slopes, poorer rocky soils, or floodplains that are periodically inundated (Bennett, 1993). Rates of clearing native vegetation over the decade 1983–1993 could be greater than 500 000 hectares per year (Noble *et al*., 1996).

Introduced species

Within this fragmented landscape exotic species have established and are continuing to adversely affect the Australian biota (Adamson & Fox, 1982). Today about one tenth of the continental vascular flora comprises species that have arrived on these shores only in the last two centuries. In some groups the proportion is higher. For example, perhaps one third of Australia's present grass flora is introduced.

After only 78 years of European settlement Woolls (1869) was able to list over 100 introduced plants occurring 'in the neighbourhood of Sydney'. Similarly, for South Australia, Schomburgk (1879) listed 99 naturalised weeds. Interestingly, this included 14 species which were introduced as garden plants and which had escaped, an unfortunate precursor of a trend that continues today.

Of the present c. 2000 naturalised species most are apparently innocuous, but many are invasive and troublesome, with 220 declared noxious weeds. Weeds are not restricted to terrestrial environments and 65 species of aquatic plants have become weeds of inland waters as a result of intentional or accidental release from aquaria. As well, there are many introduced algae which are now prolific in Australian coastal communities. The most notable, Japanese kelp (*Undaria pinnatifida*) was probably introduced accidentally with the discharge of ballast waters. Introduced fungi have also had a detrimental impact on Australia's flora. The introduced root pathogen *Phytophthora cinnamomi* has severely impacted on the vegetation, particularly in south-western Western Australia. Members of the families Proteaceae and Epacridaceae are particularly susceptible and some species may go extinct as a result of the infection (Wills, 1993).

Most sandy beaches along the east coast of New South Wales now include the South African plant *Chrysanthemoides monilifera* subsp. *rotundata* (Bitou bush) in the dune vegetation. Abandoned dairy farms on the north coast of New South Wales are marked by the presence of large *Cinnamomum camphora* (Chinese camphor laurel) trees. The site of abandoned inland homesteads is now often only marked by the Chilean pepper trees (*Schinus molle*) once grown for shade but now naturalised.

Potential weedy plant species continue to be introduced to Australia. Intentional introductions include pasture plants. Between 1947 and 1985 463 exotic pasture grass and legume species were introduced to northern Australia (Lonsdale, 1994). Of these, only four species were subsequently found to be useful, 43 became listed weeds, while another 17 were found useful but weedy.

Disturbance

Disturbance is an integral part of ecosystem function and indeed maximum biodiversity occurs at intermediate levels of disturbance (Petraitis *et al.*, 1989). The response of any community to a disturbance rests on the life history of the constituent species and in particular on the time to reproductive maturity after disturbance (Noble & Slatyer, 1980). Disturbance has been shown to affect both alpha diversity and beta diversity (Turner, 1987). Alpha diversity is conventionally given as the number of species in 0.1 hectare (Rice & Westoby, 1983). Beta diversity measures the change in composition as one moves across the landscape. In particular, habitat fragmentation affects disturbance regimes and promotes 'edge' species (Hobbs, 1987). Disturbance is known to increase the invasibility of communities (M.Fox & B.Fox, 1986a; Hobbs, 1991).

The ability of a community to return to its pre-disturbance composition is referred to as resilience (Westman, 1978, 1986). The concept that communities or ecosystems can be stressed beyond their resilience capacity, and instead reach a new steady-state has been suggested (Adamson & Fox, 1982). These aspects of disturbance to and invasion of animal and plant communities have been reviewed by B.Fox & M.Fox (1986), M.Fox & B.Fox (1986a), and Hobbs (1989).

In many contemporary situations, especially in fragmented landscapes, multiple disturbances impact on remnant native vegetation. For example, settlement patterns in the northern suburbs of Sydney have preferentially moved out along plateaus and ridgetops, leaving natural vegetation in the gullies between. Runoff from urban areas upslope brings extra water and nutrients to the gullies. In the moister, richer soils invasive plant species, particularly those dispersed by birds, find ideal growing conditions. As a result, the vegetation of gullies now includes many garden escapes such as *Cotoneaster*, *Impatiens*, *Tradescantia*, and Small-leaved privet (*Ligustrum sinense*) in addition to some native species that have expanded their range, exploiting the new resources. An example of such a weedy native species is Sweet Pittosporum (*Pittosporum undulatum*). The disturbance operating is a combination of a reduction in fire frequency in wet gullies adjacent to densely settled urban areas combined with altered nutrient and moisture levels.

Disturbance by introduced vertebrates can have profound influences on soils, and indirectly on vegetation. All of these cause changes in ecosystem function: hard-hoofed animals break up the duricrust of arid soils, disrupting algal and lichen mats, which in turn affects water infiltration rates and soil hydrology. Browsers, such as goats, break shrub branches and alter the architecture of structurally-important components of plant communities. They also concentrate their urine and faeces in localised areas and cause nutrient-rich 'hot spots' in the environment. Pigs cause considerable physical damage to plants of waterways, exposing roots and increasing turbidity. The rabbit causes localised disruption by creating warren complexes which are deeply excavated and laterally extensive; they undermine shrubs, have latrines where urine is concentrated, and create runways which are trampled and on which water cannot penetrate. All of these simultaneously adversely impact on native plant species and create habitat more suited to exotic species.

Introductions affecting ecosystem functioning

Invasive weeds that become dominant and transform aspects of ecosystem function have been termed 'transformer species' (Wells *et al.*, 1986). Transformer species irreversibly alter habitats or landscapes, i.e. they change the character, condition, form or nature of a natural ecosystem over a substantial area (Wells *et al.*, 1986). Vitousek *et al.*, (1996) suggested three main ways in which such species are effective: some alter resource levels, as in the case of nitrogen-fixing plants, others alter trophic structure, particularly by adding a new predator, and a third group alter the disturbance regime, as, for example, some introduced grasses which alter the fire regime. Four examples of transformer species in inland Australia are given below, but many others could be cited:

Athel Pine or Salt-Cedar (*Tamarix aphylla*), introduced from Eurasia as a shade tree, has spread along the Finke River system in central Australia, changing siltation patterns, soil salinity, wildlife habitats and displacing the native River Red Gum (*Eucalyptus camaldulensis*). *Tamarix* also lowers the water table, sucking water holes dry, and is a nitrogen-fixer, altering nutrient cycling and status of soils. It has the potential to spread throughout arid Australian river systems (Griffin *et al.*, 1989; Humphries *et al.*, 1991). Congeners of this invasive tree have also spread over the arid zone of North America with severe impacts on flora, wildlife and fluvial geomorphology (Loope *et al.*, 1988).

Prickly Acacia (*Acacia nilotica*), a highly invasive small tree from the Middle East, is spreading uncontrolled across the indigenous grasslands (*Astrebla* spp.) in central Queensland, northern New South Wales and is in the Barkly Tablelands of the Northern Territory. When canopy cover of the tree exceeds 50% it excludes perennial native grasses, which are replaced by annual grasses and bare soil. This alteration to the spatial patterning in the community consequently alters fire behaviour. It is considered a threat to this biome continent-wide (Humphries *et al*. 1991).

Mesquite (*Prosopis* spp.) is a seriously invasive tree that has a very deep and extensive root system and competes strongly with native species for available water. At present it is restricted to parts of Queensland, western New South Wales, South Australia and Western Australia, but could spread through much of inland Australia (Humphries *et al.*, 1991). In the United States of America where it is native Mesquite has expanded its range to cover over 28 million hectares. Mesquite is also invasive of arid communities in southern Africa (Brown & Gubb, 1986).

Buffel Grass (*Cenchrus ciliaris*), widely planted for pastoral purposes throughout arid and semi-arid Australia, is displacing native species and altering fire regimes in moister habitats (Humphries *et al.*, 1991).

In all cases of successful introductions of subsequently significant transformer species, it may be difficult to determine if the conditions that led to the introduction also contribute to the alteration of ecosystem function after the establishment of the invader. Where the invasion is relatively recent it is easier to determine this, although it may not always be possible. In the case of *Tamarix aphylla* cause and effect can be established. Its spread in central Australia is dated from the exceptionally wet year of 1974 (Griffin *et al.*, 1989). The trigger for its spread was climatic, source material (seed and mature plants for coppicing) was available, and the habitat not fully occupied (presumably). The results of its successful establishment, which involve alteration to ecosystem function, include changes to thevegewtation by:

- displacement of native tree species,
- formation of monospecific stands,
- promotion of salt-tolerant understorey, and
- displacement of diverse native herbaceous understorey.

In addition there are changes in browse for both stock and native herbivores because the foliage is highly saline and is not palatable to stock nor to native invertebrate foliovores. The litter that accumulates is thick, packed, saline needle litter, which leads to a depauperate leaf litter invertebrate fauna. There are also fewer logs and branches. The altered community contains fewer birds and reptiles. Nutrient cycling is altered because of nitrogen fixation by the *Tamarix*. Associated hydrological changes include:

- reduced channel width,
- increased sedimentation,
- altered stream hydrology,
- lowered water table (Griffin *et al.*, 1989; Humphries *et al*, 1991).

All of these constitute changes to ecosystem function, or loss of biodiversity, and were not the environmental change that contributed to the initial spread of the invading species.

Some native species have been positively affected by disturbance associated with land-use practices. Some opportunistic native species behave like weeds. For example the Native Thornapple (*Datura leichhardtii*) is a native species which spread with the introduction of large grazing animals and with the soil disturbance they cause, and is now declared a noxious weed. In semi-arid and arid woodlands and shrublands, grazing by livestock, kangaroos and feral goats has thinned the perennial native grass cover which, together with fewer fires, has resulted in prolific growth of 'woody weeds' (Noble *et al*., 1996). These weeds are mainly native species of *Eremophila, Cassia/Senna, Pittosporum*, and other native shrubs which would normally be fairly inconspicuous members of the community.

Land use and land tenure

Of the land area of Australia, cities and towns now occupy approximately 0.01%, mining operations a similar area (0.01%), surface waters 3%, crops 6%, conservation reserves 7%, unused land 9% and rangelands 75% (Noble *et al*., 1996). The principal land use in Australia is agriculture (Table 14), with grazing by cattle and sheep being the most extensive form of agricultural pursuit. Australia's arable land comprises 467 000 km^2 and much of this area has been cleared of natural vegetation and converted to croplands (Graetz *et al*., 1995).

The area of the continent used in some form of agricultural pursuit is 61% (Australian Bureau of Statistics, 1992a, Table 14). Of this area, most is used for grazing, a land-use in which some elements of the native vegetation do persist but where exotic species have established extensively. An area of almost 50 million hectares has been converted to either crops or sown pastures; both land uses replace native vegetation. A smaller area (42 million hectares) is used for forestry pursuits, only a very small proportion of which is for plantations. Native forests retain many of the native plant species, although the degree of 'naturalness' is dependent on local management practices.

Table 14. Land use in Australia.
(Data from Australian Bureau of Statistics, Year Book Australia, 1992a).

Land use	Area (× 10^6 ha)	Percentage
Agriculture (total)	466.6	60.8
Crops	17.0	2.2
Sown pasture	30.9	4.0
Grazing	418.7	54.5
Forestry (total)	41.84	5.5
Native forest	40.8	5.4
Plantation	1.04	0.1
Protected areas (wilderness, national parks, conservation reserves, etc)	36.5	4.8
Urban and unused (incl. vacant crown land)	223.06	29.0
Total Australian land area	768.0	100.0

The data in Table 14 for the conservation estate ('protected areas') date from 1989. In almost a decade this area has increased significantly, much of the newly acquired land being taken from the 'unused' category of vacant crown land. Overall, the total conservation estate in 1995 (534 900 km^2 or 53.49 × 10^6 ha) is 7% of the land area of the country, well below the OECD average of 9.1% (Organisation for Economic Cooperation and Development, 1995). Australia lags behind other similar sized OECD countries such as Canada (8.9%) and the

USA (10.6%); New Zealand has 22.8% of its area in formal reserves. See Cresswell (this volume) for a more extensive discussion of conservation.

Today only 13% of Australia's land is privately held as freehold title (Bureau of Agricultural Economics, 1983). Almost 5 million km^2 or 63% of the land area is private land, as crown lease or freehold (AUSLIG, 1993b). However Australia is unique among the developed nations in having a high proportion of the land publicly owned. Of the 1.8 million km^2 of public land, most (54%) is Vacant Crown Land. Only about 30% is in the conservation estate (AUSLIG, 1993b). Western Australia has over 60% of the nation's public land, most of this as Vacant Crown Land (Table 15) while the Australian Capital Territory has less than 1% of public land. Most of the nature conservation lands are in South Australia and Western Australia. The bulk of Australia's extensive natural vegetation resides on these public lands but its continued existence is predicated on appropriate management.

Plant biodiversity is threatened by land-use practices that lead to vegetation clearing and increased grazing (predation). Of the 87 plant species presumed extinct, over half previously occurred in areas now cleared for agriculture (Leigh & Briggs, 1994). Table 16 indicates the major causes of extinctions and the past and present threats to endangered plant species.

Table 15. The amount of public land in '000 square kilometres, classified into nine categories for each of the States and Territories, with the percentage of each category for the entire State shown in parentheses. The total amounts of public land for each category are shown as row total (with the percentage of all public lands in Australia in parentheses). The total amount of public land for each state is shown as column totals (with the percentage of all public lands in Australia shown in parentheses). (Based on information in AUSLIG 1998).

Public Land Category	QLD	NSW	VIC	SA	WA	NT	TAS	ACT	Total for each category (%)
Vacant Crown Land	0.6 (0.51)	1.4 (1.6)	-	8.3 (3.8)	863.3 (78.8)	82.8 (60.4)	4.3 (10.6)	-	960.7 (54.3)
Other Crown land	13.9 (11.8)	6.4 (7.5)	2.0 (2.8)	0.8 (0.4)	42.7 (3.9)	12.3 (9.0)	2.5 (6.2)	-	80.6 (4.6)
Nature conservation reserve	54.2 (45.9)	38.1 (44.3)	30.6 (42.3)	203.7 (93.6)	155.0 (14.2)	27.8 (20.3)	13.5 (33.3)	1.2 (80.0)	524.1 (29.7)
Aboriginal freehold-national park	-	-	-	-	-	10.8 (7.9)	-	-	10.8 (0.6)
Forestry reserve	40.1 (34.0)	34.6 (40.4)	36.4 (50.6)	1.0 (0.5)	20.9 (1.9)	-	15.1 (37.2)	0.1 (6.67)	148.2 (8.4)
Water reserve	0.3 (0.3)	2.8 (3.3)	1.5 (2.1)	0.2 (0.1)	5.3 (0.5)	-	0.9 (2.2)	-	11.0 (0.6)
Defence land	3.8 (3.2)	0.4 (0.5)	0.4 (0.6)	3.6 (1.7)	6.6 (0.6)	3.5 (2.6)	0.3 (0.7)	-	18.6 (1.1)
Mining reserve	4.3 (3.6)	-	0.3 (0.4)	-	0.4 (0.04)	-	-	-	5.0 (0.3)
Mixed category	0.8 (0.7)	2.0 (2.3)	1.1 (1.5)	-	0.8 (0.07)	-	4.0 (9.9)	0.2 (13.3)	8.9 (0.5)
Total for each State (%)	118.0 (6.7)	85.7 (4.8)	72.3 (4.1)	217.6 (12.3)	1095.0 (61.9)	137.2 (7.8)	40.6 (2.3)	1.5 (0.08)	1767.9 (100.0)

Table 16. Extinct and endangered plant species: major causes of extinction and past and present threats to endangered plant species (data from Leigh & Briggs, 1994).

Threat/cause	No. of species presumed extinct	No. of endangered species (past threat)	No. of threatened species (present and future threat)
Agriculture	44	112	50
Grazing	34	51	55
Low numbers	-	10	85
Weed competition	4	12	57
Roadworks	1	8	57
Industrial/urban development	3	20	21
Fire frequency	-	10	17
Forestry	-	10	10
Collecting	-	6	17
Mining	1	3	11

Many species are affected by more than one threat and in some cases past threats may no longer operate and new ones have arisen. Other threats not listed in the table are recreation, dieback, railway maintenance, salinity, insect attack, quarrying, trampling by pigs and buffalo, drainage and flooding (Leigh & Briggs, 1994). When other potential threats, such as those accompanying climate change are also invoked, there are considerable grounds for holding grave concern for the future of Australia's flora and native vegetation. However in the last decade or so, heightened public awareness of the environment, and of the importance of conservation to the future of life on the planet, including our own, gives cause for optimism that historical processes of degradation and species loss can be slowed and halted.

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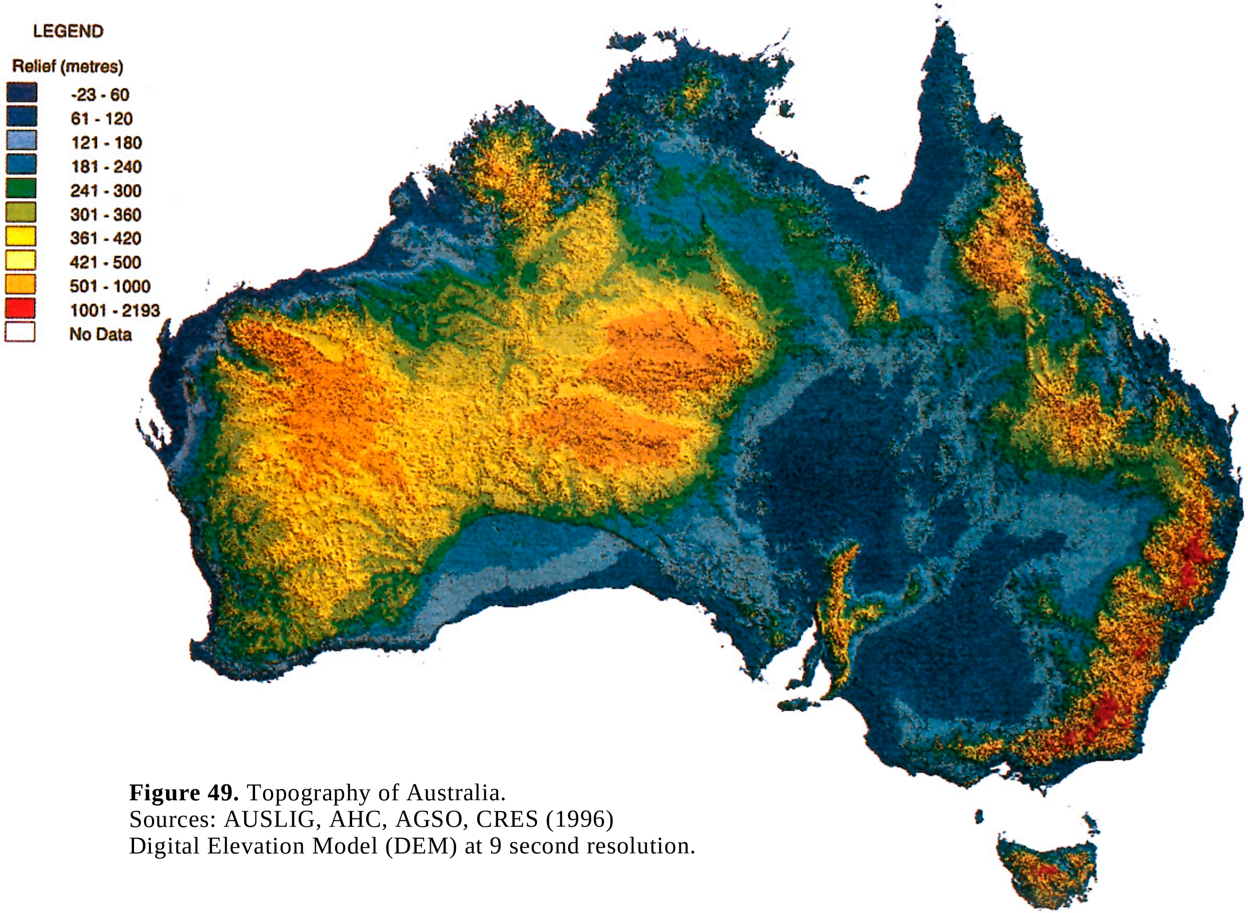


Figure 49. Topography of Australia.
Sources: AUSLIG, AHC, AGSO, CRES (1996)
Digital Elevation Model (DEM) at 9 second resolution.

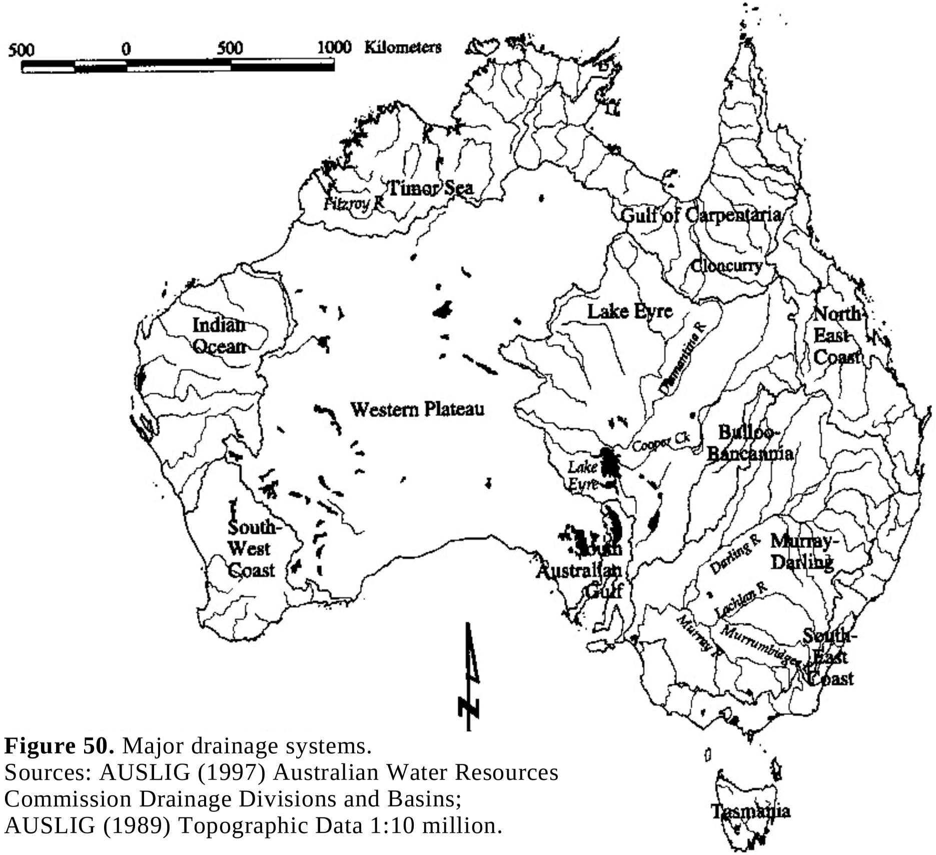


Figure 50. Major drainage systems.
Sources: AUSLIG (1997) Australian Water Resources Commission Drainage Divisions and Basins;
AUSLIG (1989) Topographic Data 1:10 million.

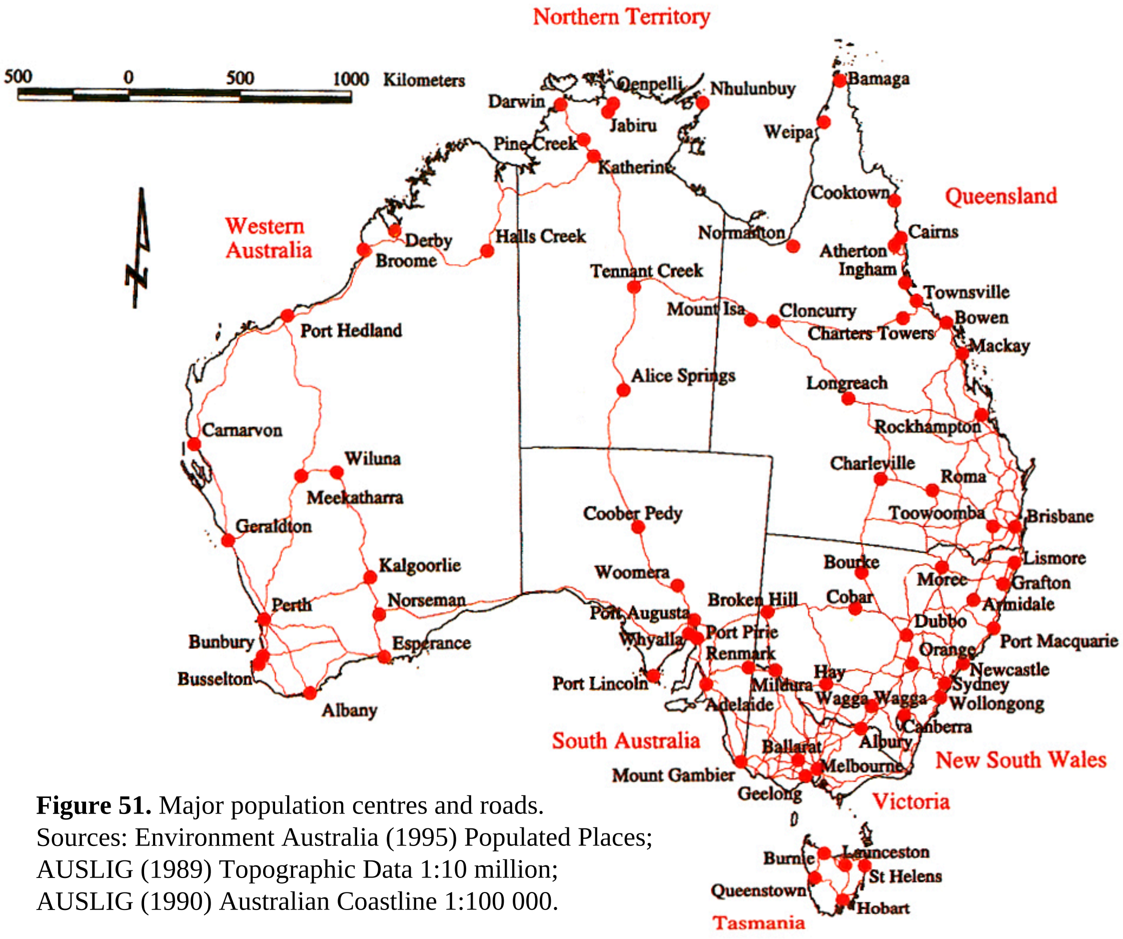
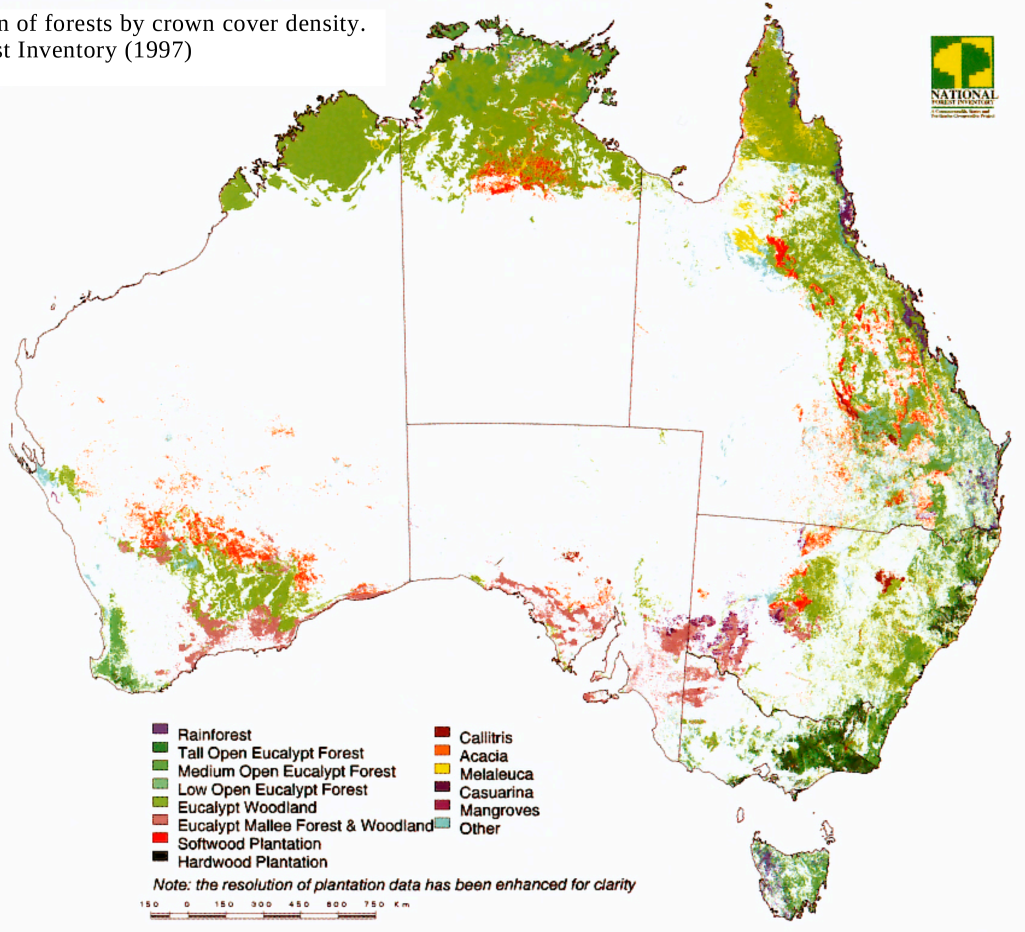


Figure 51. Major population centres and roads.
Sources: Environment Australia (1995) Populated Places;
AUSLIG (1989) Topographic Data 1:10 million;
AUSLIG (1990) Australian Coastline 1:100 000.

Figure 52. Distribution of forests by crown cover density.
Source: National Forest Inventory (1997)


NATIONAL FOREST INVENTORY
Rainforest
Tall Open Eucalypt Forest
Medium Open Eucalypt Forest
Low Open Eucalypt Forest
Eucalypt Woodland
Eucalypt Mallee Forest & Woodland
Softwood Plantation
Hardwood Plantation
Callitris
Acacia
Melaleuca
Casuarina
Mangroves
Other
Note: the resolution of plantation data has been enhanced for clarity
150 0 150 300 450 600 750 Km

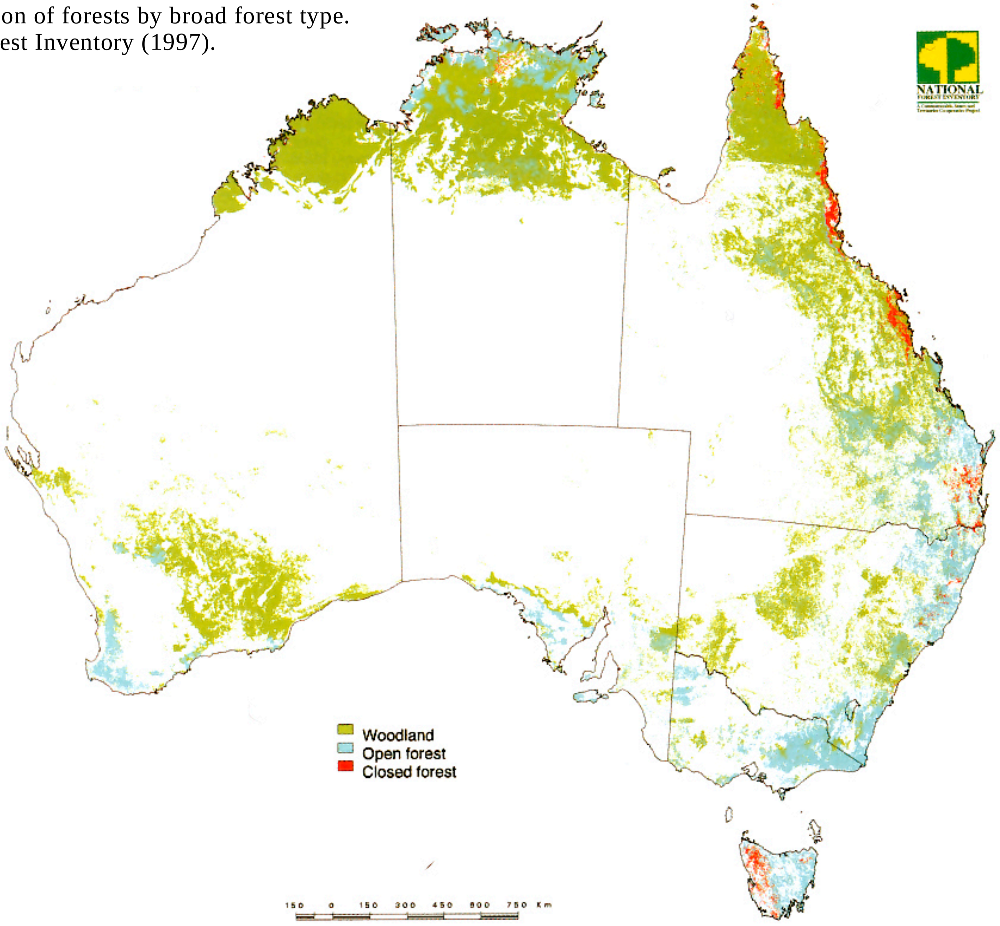
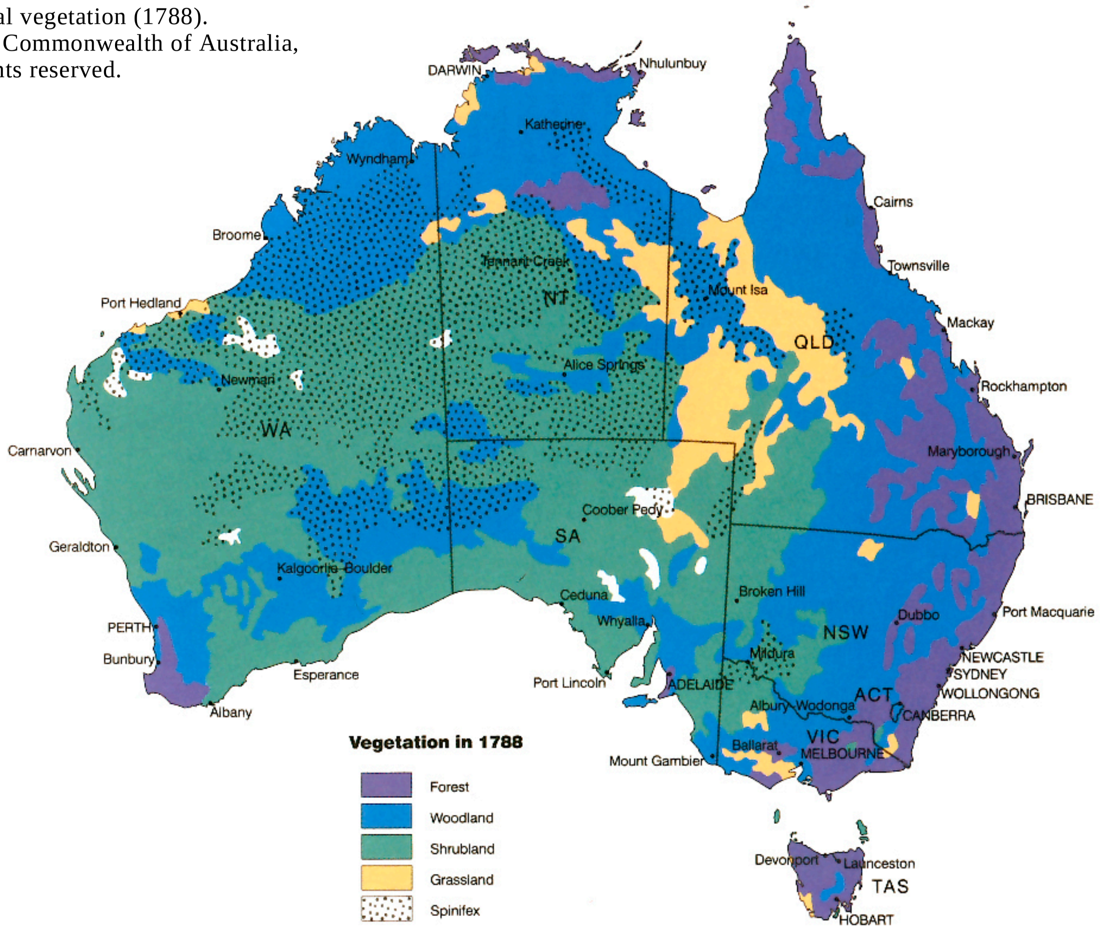


Figure 53. Distribution of forests by broad forest type.
Source: National Forest Inventory (1997).

Figure 54. Natural vegetation (1788).
Map copyright © Commonwealth of Australia, AUSLIG. All rights reserved.



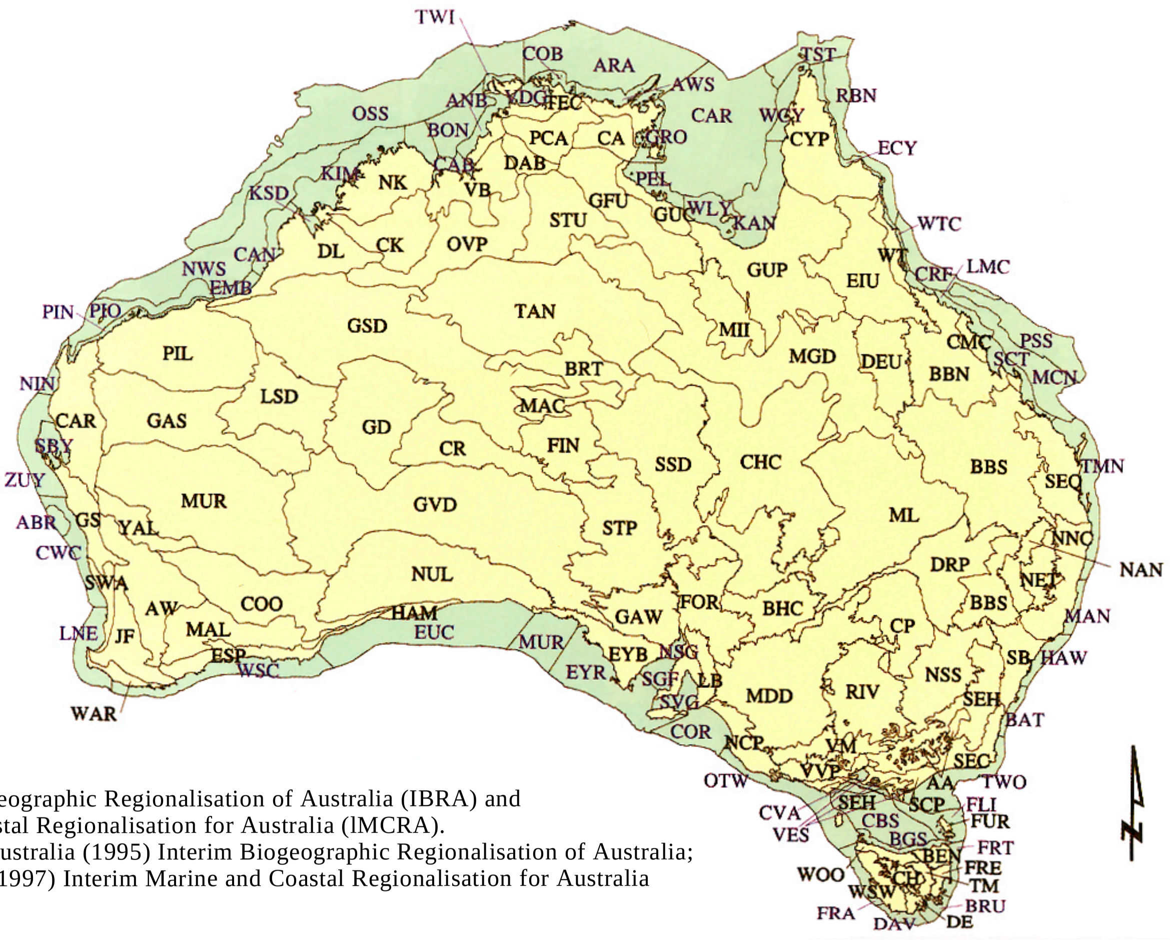


Figure 55. Interim Biogeographic Regionalisation of Australia (IBRA) and Interim Marine and Coastal Regionalisation for Australia (IMCRA).
Sources: Environment Australia (1995) Interim Biogeographic Regionalisation of Australia; Environment Australia (1997) Interim Marine and Coastal Regionalisation for Australia (Mesoscale).

Legend to IBRA/IMCRA regions in Figure 55.

IBRA code	IBRA name
AA	Australian Alps
AW	Avon Wheatbelt
BBN	Brigalow Belt North
BBS	Brigalow Bell South
BEN	Ben Lomond
BHC	Broken Hill Complex
BRT	Burt Plain
CA	Central Arnhem
CAR	Carnarvon
CH	Central Highlands
CHC	Channel Country
CK	Central Kimberley
CMC	Central Mackay Coast
COO	Coolgardie
CP	Cobar Peneplain
CR	Central Ranges
CYP	Cape York Peninsula
DAB	Daly Basin
DE	D’Entrecasteaux
DEU	Desert Uplands
DL	Dampierland
DRP	Darling Riverine Plains
EIU	Einasleigh Uplands
ESP	Esperance Plains
EYB	Eyre and Yorke Blocks
FIN	Finke
FOR	Flinders and Olary Ranges
FRE	Freycinet
FUR	Furneaux
GAS	Gascoyne
GAW	Gawler
GD	Gibson Desert
GFU	Gulf Fall and Uplands
GS	Geraldton Sandplains
GSD	Great Sandy Desert
GUC	Gulf Coast
GVD	Great Victorian Desert
HAM	Hampton
JF	Jarrah Forest
GUP	Gulf Plains
LB	Lofty Block
LSD	Little Sandy Desert
MAC	MacDonnell Range
MAL	Mallee
MOD	Murray-Darling Depression
MGD	Mitchell Grass Downs
ML	Mulga Lands
MUR	Murchison
NAN	Nandawar
NCP	Naracoorte Coastal Plain
NET	New England Tableland
NK	Northern Kimberley
NNC	NSW North Coast
NSS	NSW South western Slopes
NUL	Nullarbor
OVP	Ord-Victoria Plains
PCA	Pine-Creek Arnhem
PIL	Pilbara
RIV	Riverina
SB	Sydney Basin
SCP	South east Coastal Plain
SEC	South East Corner
SEH	South Eastern Highlands
SEQ	South Eastern Queensland
SSD	Simpson-Strzelecki Dunefields
STP	Stony Plains
STU	Sturt Plateau
SWA	Swan Coastal Plain
TAN	Tanami
TEC	Top End Coastal
TM	Tasmanian Midlands
VB	Victoria Bonaparte
VM	Victorian Midlands
VVP	Victorian Volcanic Plain
WAR	Warren
WOO	Woolnorth
WSW	West and South West
WT	Wet Tropics
YAL	Yalgoo

IMCRA Code	IMCRA name
ABR	Abrolhos Islands
ANB	Anson Beagle
ARA	Arafura
AWS	Arnhem Wessel
BAT	Batemans Shelf
BGS	Boags
BON	Bonaparte Gulf
BRU	Bruny
CAB	Cambridge-Bonaparte
CAN	Canning
CAR	Carpentaria
COB	Cobourg
COR	Coorong
CRF	Central Reef
CVA	Central Victoria
CWC	Central West Coast
DAV	Davey
ECY	East Cape York
EMB	Eighty Mile Beach
EUC	Eucla
EYR	Eyre
FLI	Flinders
FRA	Franklin
FRT	Freycinet
GRO	Groote
HAW	Hawkesbury Shelf
KAN	Karumba-Nassau
KIM	Kimberley
KSD	King Sound
LMC	Lucinda-Mackay Coast
LNE	Leeuwin-Naturaliste
MAN	Manning Shelf
MCN	Mackay-Capricorn
MUR	Murat
NIN	Ningaloo
NSG	North Spencer Gulf
NWS	North West Shelf
OSS	Oceanic Shoals
OTW	Otway
PEL	Pellew
PIN	Pilbara (nearshore)
PIO	Pilbara (offshore)
PSS	Pompey-Swains
RBN	Robbins
SBY	Shark Bay
SCT	Shoalwater Coast
SGF	Spencer Gull
SVG	St Vincent Gulf
TMN	Tweed-Moreton
TST	Torres Straits
TWI	Tiwi
TWO	Twofold Shelf
VDG	Van Diemens Gulf
VES	Victorian Embayments
WCY	West Cape York
WLY	Wellesley
WSC	WA South Coast
WTC	Wet Tropic Coast
ZUY	Zuytdorp

EVOLUTION OF THE AUSTRALIAN FLORA: FOSSIL EVIDENCE

Robert S. Hill[1], *Elizabeth M. Truswell*[2], *Stephen McLoughlin*[3] & *Mary E. Dettmann*[4]

Evolution of life in the Precambrian

The Precambrian accounts for a large proportion of the history of the Earth and incorporates most, if not all, of the major evolutionary events in the history of life (Fig. 56). It was the time of the origin of life itself, photosynthesis (and later oxygenic photosynthesis), eukaryotic organisation, and multicellular (including megascopic) life. By the close of the Precambrian, algal life was relatively well developed, and may even have made the transition to a terrestrial existence between 2200 and 1800 million years ago, as soon as the ozone shield was well-established (Beeunas & Knauth, 1985).

The origin of life

Australia is an ancient continent, and has an excellent Precambrian record. Some of the events mentioned above are recorded in Australian Precambrian sedimentary rocks. The time of the origin of life is still very uncertain, but it seems reasonable to assume that the only early constraint (excluding an extraterrestrial source for life) is the Earth's attainment of a solid crust and liquid water. That the Earth had a solid crust by 4275 million years ago is shown by the discovery of detrital zircon crystals of that age from the Jack Hills Metasedimentary Belt of Western Australia (Compston & Pidgeon, 1986). It has long been argued that catastrophic meteorite bombardment probably prevented the long term establishment of life until about 3900 to 3850 million years ago. This argument claims that before this time the formation of 1000 km diameter craters released so much energy that the oceans would have been repeatedly vaporised and the planet sterilised (Chyba, 1993). Therefore, although life could have existed from the time of a solid crust, about 4275 million years ago, extant life, which is almost certainly the result of a single origin, might represent a more recent event, postdating 3900 to 3850 million years ago.

The young age constraint on the origin of life is also in dispute. Living organisms differentially assimilate stable carbon isotopes, hence $^{12}C/^{13}C$ ratios differ between carbonaceous material of biological and non-biological origin. There is some carbon isotopic evidence for the existence of autotrophic life at 3800 million years, but these data come from strongly metamorphosed rocks in Greenland and are widely considered to be unreliable, since carbon isotopes are reset during high-grade metamorphism and the correction factors necessary to readjust data to original values are poorly established (Schopf, 1983; Schopf & Klein, 1992). Thus in order to be certain about a young age constraint on the origin of life it is necessary to look for the oldest mildly metamorphosed rocks. Low grade greenstones in the Pilbara Craton in Western Australia, approximately 3500 million years old, seem to have accumulated on crust that was already rigid, cool and buoyant (Buick *et al*., 1995). These rocks have only ever been heated to approximately 350–400°C, a temperature at which carbon isotopic data are still reliable. These rocks may prove critical to constraining the origins of life on Earth, since they can be tested for evidence of the characteristic fractionation imparted by autotrophic carbon fixation (R.Buick, *pers. comm*.).

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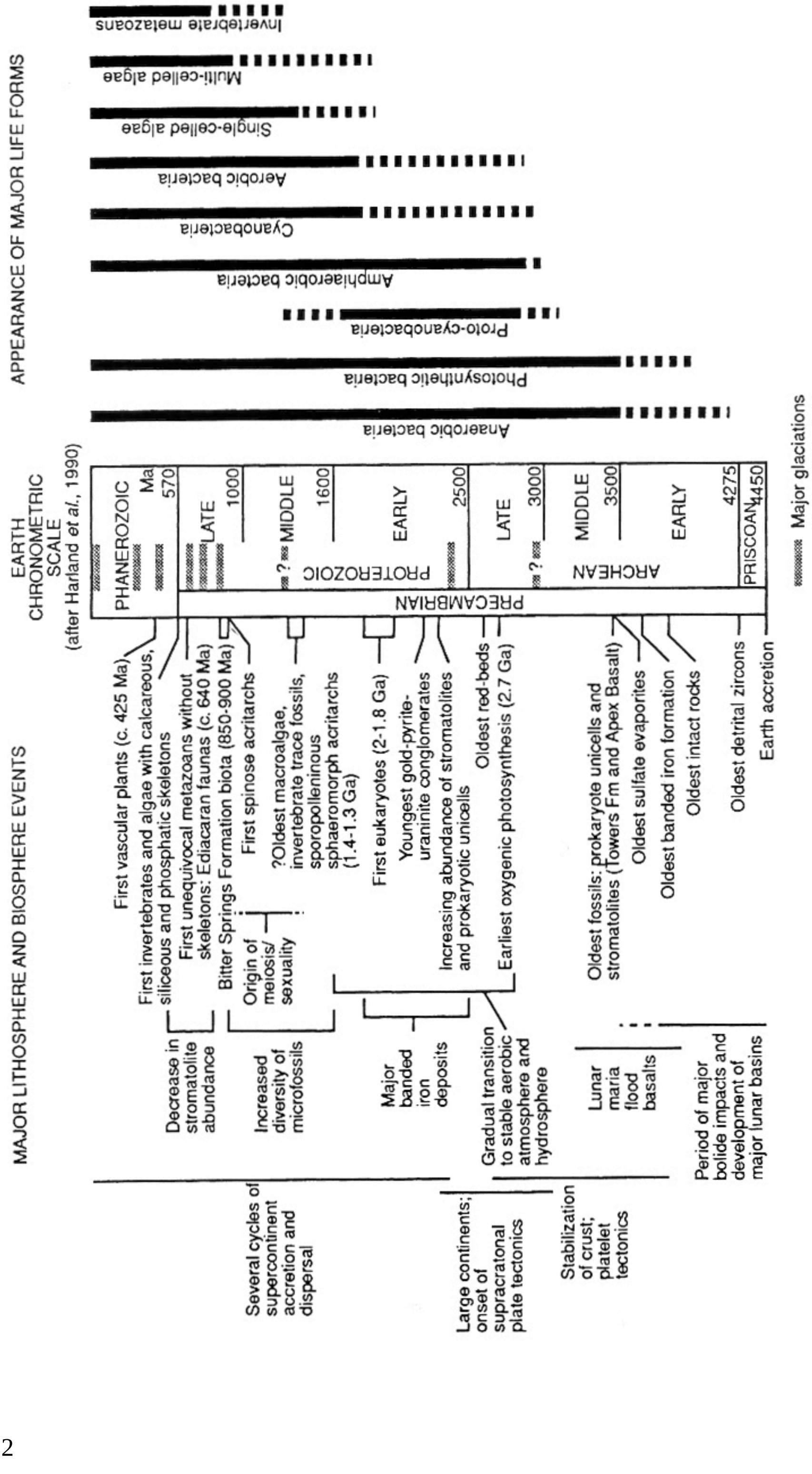

Figure 56. Major biological and geological events in early Earth history (modified from Schopf *et al.* 1983).

Photosynthesis

The earliest evidence for photosynthetic life is found in Australia and is dated at 3460 million years ago. Filamentous microfossils have been found in the Pilbara region (within the Towers Formation and Apex Basalt of the Warrawoona Group) that resemble cyanobacteria, although they also resemble non-photosynthetic gliding bacteria, so their morphology is not definitive (Schopf, 1992). Nevertheless, Schopf considered that these microfossils meet the three tests required to confirm the presence of early life: they are not contaminants, the geologic source of the rocks is known with certainty, and they are definitely the remains of ancient organisms rather than being, for example, 'biologic-shaped' mineral grains. Numerous different types of fossil filaments have been discovered in the Pilbara cherts, and their morphology matches that of living prokaryotic organisms very closely.

Stronger evidence for photosynthesis comes from stromatolites, dome-shaped sedimentary structures built up by phototropic micro-organisms. Stromatolites are the least controversial evidence of early life, since they are still extant today, with perhaps the best known examples occurring not far from the earliest fossils at Shark Bay in north-western Australia. Walter *et al*. (1980) described stromatolites from North Pole in north-western Australia (Warrawoona Group) that are between 3460 and 3520 million years old. These represent the oldest substantial evidence for life in the fossil record to date, although Schopf (1992) noted that the absence of micro-organisms with cellular preservation, while not surprising, leaves open the possibility of a non-biological origin. Although Walter *et al*. (1980) stressed that the presence of these stromatolites did not confirm the presence of oxygen-producing photosynthesis, they are associated with sedimentary sulphate minerals, which, given the reduced or neutral composition of the early atmosphere, can only have been produced as by-products of photosynthesis, either oxygenic or sulphur-oxidising (R.Buick, *pers. comm*.). The composition of the atmosphere during this time is still uncertain, since many recent attempts at modelling it suggest that it contained low levels of oxygen (Schopf, 1983).

In extremely ancient rocks it is impossible to tell what kind of photosynthesis was operating, and it is not until approximately 2715 million years ago that there is clear evidence of oxygenic photosynthesis of the type now employed by plants. This evidence also comes from the Pilbara region of Western Australia. There, in stromatolites that clearly grew within saline lakes, there is an odd succession of evaporite minerals that indicate sedimentary sulphate was not one of the by-products of photosynthesis. This leaves only oxygenic photosynthesis as the primary source of carbon fixation for the local biota (Hayes *et al*., 1983; Buick, 1992).

Eukaryotic organisation

All fossilised life forms from the early part of the Precambrian (Archean) are accepted as being prokaryotic, i.e. non-nucleated bacteria and cyanobacteria or their extinct relatives. A major step in the evolution of life was that from the prokaryotic to the eukaryotic condition, in which cells have a membrane-bound nucleus and organelles. This was a profound evolutionary event, allowing for the later appearance of all multicellular organisms. It is now generally accepted that the origin of eukaryotes involved the ingestion but not digestion of one set of prokaryotes by another, leading to such elegant symbioses that the process has only recently been widely recognised (Margulis & Sagan, 1986) after first being suggested early this century (Wallin, 1927).

The time of origin of eukaryotic organisation is difficult to determine, since the earliest eukaryotes were presumably simple unicells, similar in size and shape to co-occurring prokaryotes. The profound difference was the presence of membrane-bound organelles in the former, but recognition of this feature in fossils is problematic at best. Early eukaryotes can therefore only be determined with confidence in the fossil record if they had evolved substantially away from their prokaryotic ancestors. There is some indirect evidence to constrain the earliest appearance of eukaryotes. Most of them are strict aerobes, and thus it seems unlikely that they would have been widespread prior to the appearance of a global aerobic environment, somewhere between 1850 and 2200 million years ago (Holland & Beukes, 1990). The evidence for a transition from anaerobic to aerobic conditions during the

Palaeoproterozoic, about 2000 million years ago, derives chiefly from sedimentological features. Uraninite (UO_2) and pyrite (FeS_2) are common detrital components of Archean sedimentary rocks, but under oxidising conditions these minerals rapidly break down and are rare after the early part of the Proterozoic and in younger sediments. Conversely, terrestrial red-beds rich in haematite (Fe_2O_3) develop under oxidising conditions and are widespread only in post-Palaeoproterozoic sedimentary sequences. Banded iron formations contain a large proportion of haematite and formed predominantly around 2500–1800 million years ago, the period that probably corresponded to the transition to a consistently oxidising atmosphere (Fig. 56). Significantly, the abundance of stromatolites in the fossil record increases markedly in the Early Proterozoic (around 2300 million years ago).

Living spheroidal cyanobacteria, the largest coccoid prokaryotes, are generally less than 10 μm in diameter, although a few species are as large as 60 μm (Schopf, 1992). In contrast, living eukaryotic microalgae tend to have much larger cells, and thus there is a clear cell size differential apparent today which can be used to infer the cell type of fossils. According to Schopf (1992), the size range of fossil coccoid cells detected thus far in the early Proterozoic shallow-water stromatolitic units are within the prokaryotic size range, and thus probably do not include eukaryotes. However, offshore (deeper water) shales contain much larger cells, including possible eukaryotes, by 2000 million years ago, and assured eukaryotes by 1800 million years ago. According to Knoll (1992), these simple, spheroidal microalgae constitute the oldest evidence yet detected of the eukaryotic cell type.

Diverse types of planktonic, eukaryotic microalgae are now known from the later Proterozoic, but their exact biological relationships are unknown. For this reason, they are known as acritarchs, from the Greek *akritos* = doubtful, and *arche* = origin (Traverse, 1988). Relatively small sphaeromorph acritarchs (between 60 and 200 μm in diameter) are abundant from the Mesoproterozoic onwards, but truly large sphaeromorphs, more than a millimetre in diameter, are typical only of the Neoproterozoic, from about 1000 to about 675 million years ago (Zang & Walter, 1989, 1992; Schopf, 1992). The reason for the rise to prominence and subsequent decline of acritarchs is not yet fully understood. However, environmental fluctuations associated with extensive Late Proterozoic glaciations, competition from other newly emerging algal groups, and predation resulting from marked diversification of heterotrophic organisms towards the close of the Proterozoic were probably all significant factors influencing acritarch abundance (Fig. 56).

Precambrian rocks that are critical to our understanding of the evolution of eukaryotic life occur in the approximately 800 million year old Bitter Springs Formation of central Australia (Schopf, 1968; Schopf & Blacic, 1971; Oehler, 1976; Taylor & Taylor, 1993). Thirty taxa of microfossils have been described from these extraordinary cherts, including cyanobacteria, fungus-like filaments which are probably cyanobacterial sheaths, and possible Pyrrophyta and spheroidal green algae in which nuclear residues, pyrenoid-like bodies and other cellular structures were considered to have been cytologically preserved (Schopf, 1968). However, the identification of preserved organelles in these microfossils continues to generate controversy (Taylor & Taylor, 1993), with most workers now regarding these intracellular structures as remnants of degraded cytoplasm (Knoll & Barghoorn, 1975).

Multicellular life

The transition from unicellular to multicellular life clearly represents a critical phase in the evolution of both plant and animal life, although multicellularity is not restricted to those organisms. However, the fossil record is, at present, unhelpful in interpreting this transformation, and we are left to rely on several well-presented, but largely untested, hypotheses for this very significant transition. The fossil record contains quite a number of Precambrian multicellular fossils, the oldest certain example being of a bangiophyte red alga from Canada, about 1260 to 950 million years old (Butterfield *et al.*, 1990). However, impressions of a possible multicellular brown alga like *Hormosira* have been found in Mesoproterozoic rocks of the Bangemall Group of Western Australia (Grey & Williams, 1990) and compressions of megascopic, possibly multicellular algae have recently been found in 2100 million year old rocks from Minnesota (Han & Runnegar, 1992). At timescales of 750 to 700 million years ago a wide range of multicellular organisms are found in the Svanbergfjellet Formation of Spitsbergen, including simple coenocytic and coenobial forms, and truly multicellular forms showing significant cellular differentiation (Butterfield *et al*., 1994).

Relevant to the evolution of multicellularity in plants is the recent reinterpretation of the Ediacaran 'fauna' by Retallack (1994). The Ediacaran fossils, originally described from Ediacara in central South Australia, but now known from several localities around the world, have usually been interpreted as multicellular animals of varying affinities, and no doubt many of them are. However, Retallack (1994) has hypothesised that some of the organisms may in fact have been lichens, and as such had at least some eukaryotic algal component. This interpretation is controversial (Waggoner, 1995), and it is too early to determine whether it will have a lasting impact. However, it offers an interesting alternative to our current view of Precambrian life, since some of the Ediacaran organisms were up to one metre in diameter and were clearly multicellular. The proposition of a Precambrian landscape dominated by lichens of this type offers a foreign view to even the most creative of earlier hypotheses regarding the Precambrian landscape. It is certainly probable that some of the Ediacaran organisms were photosynthetic and Margulis & Sagan (1995) concluded that some of the later Ediacaran organisms were probably protoctists that photosynthesised in shallow seas.

It is certain that life diversified rapidly in aquatic environments beyond the end of the Precambrian. Multicellular algae, including some calcium carbonate-secreting (now known to occur in the latest Proterozoic; Horodyski & Mankiewicz, 1990; Grant *et al*., 1991) and reef-building forms, became common components of the marine realm. The next part of the evolutionary picture of major relevance to the terrestrial flora of Australia was the development of a land flora. It is probable that mosses and liverworts were an important part of the early land flora (Taylor & Taylor, 1993), but their fossil record in Australia is poor. The discussion here concentrates on the vascular land plants.

Australian early terrestrial floras (Silurian to Jurassic)

The pre-angiosperm floras of Australia are intimately linked to those of other Southern Hemisphere continents to which Australia was connected throughout most of the Palaeozoic and Mesozoic. Both changing continental positions and fluctuating global and regional climates are reflected in varying degrees of endemism or the cosmopolitan aspect of the floras through time. On several occasions through the late Palaeozoic and Mesozoic, gradual environmental change was punctuated by episodes of very rapid change, reflected in the plant fossil record by major extinction and radiation events.

Our knowledge of the succession of Australian floras is based on studies of plant macrofossils, palynomorphs (principally spores, pollen and algal cysts) and, to a lesser extent, the diversity and morphological characteristics of animals which fed on these plants (e.g. the increase in the proportion of grazing marsupials in the Late Tertiary and Quaternary suggests a response to a shift from closed to open forest and grassland vegetation in many areas). The plant macrofossil record is heavily biased towards plants growing in lowland environments, especially those areas experiencing rapid subsidence. This appears to be especially the case for pre-Tertiary floras. Wind and aqueous transport of spores and pollen from plants growing in non-depositional settings has ensured that in most cases a more complete picture of regional plant diversity can be gained from palynological studies. Palynomorphs also generally have the advantage of being preserved in a greater range of depositional environments, including marine settings. Nevertheless, problems remain with interpretations of the palynological record including the uncertain affinities of many spore-pollen groups in pre-Tertiary strata, the problem of excessive taxonomic splitting, and uncertainties surrounding the infraspecific morphological variation of spores and pollen produced by ancient plants.

Invasion of the land: the Late Silurian – Early Devonian Baragwanathia flora

The earliest vascular plants probably appeared during the late Early Silurian (Edwards & Fanning, 1985) based on records of fossilised dispersed spores and sporangia and small dichotomous axes with strengthening tissues. Reports of vascular plants from earlier periods based on dispersed spores, cuticles, or tracheid-like tubes (Richardson, 1985; Taylor, 1988) are less convincing, as these remains may be derived from algae or bryophytes. The earliest land plants preserved in Australia occur in Upper Silurian to Lower Devonian shallow marine sediments of Victoria. This flora contains a range of simple vascular plants assignable to the Rhyniophyta, Zosterophyllophyta, Trimerophyta, and Lycophyta. The flora is named after its most prominent element: the lycopod *Baragwanathia* (Fig. 57). Australia occupied equatorial latitudes during the mid-Palaeozoic (Smith *et al*., 1981) and records of early vascular plants outside Australia are also mostly recorded from low palaeolatitudes (Edwards & Fanning, 1985; Scotese & McKerrow, 1990), suggesting a tropical origin for land plants.

The age of the Baragwanathia flora has attracted some controversy, due firstly to the relatively 'advanced' morphology of *Baragwanathia* contrasting with its occurrence in sediments of such apparent antiquity, and secondly due to uncertainties over the age of the associated marine fauna (Garratt, 1978, 1981; Edwards *et al*., 1979; Hueber, 1983; Garratt *et al*., 1984). A Late Silurian (Ludlovian) age for the oldest Victorian fossil floras now appears most probable, based on reassessment of the biostratigraphic range of the associated graptolite species (Garratt *et al*., 1984).

Baragwanathia is the most robust plant in the Victorian assemblages and probably attained heights of up to 1 m, with axes up to 5 cm wide. Most of the preserved axes were probably transported subaerial portions of the plant (some bearing clusters of sporangia), but a few may represent prostrate or subterranean rhizomes.

Rhyniophytes like *Yarravia*, *Hedeia* and *Salopella* represent the simplest plants in the assemblage and are characterised by short unbranched or dichotomising leafless axes bearing simple terminal or subterminal sporangia (Tims, 1980; Tims & Chambers, 1984). Rhyniophytes now have uncertain phylogenetic status and may include many taxa with bryophytic affinities (Taylor, 1988). Zosterophyllophytes (represented by *Zosterophyllum*) show mainly simple dichotomous, or sometimes pseudomonopodially-branched axes, often with terminally aggregated reniform sporangia. Some zosterophyllophytes had simple spine-like enations on the axes and shared several other features in common with the lycophytes to which they are generally regarded as closely related (Taylor & Taylor, 1993).

Trimerophytes were generally more robust than rhyniophytes and zosterophyllophytes, and displayed more complex pseudomonopodial or monopodial branching patterns, circinnate vernation, and recurved sporangia clustered on the terminal axes. Spindle-shaped sporangia, sometimes attached to fragmentary, dichotomously branched axes assigned to *Dawsonites* (of presumed trimerophyte affinities) are common within the Victorian Upper Silurian to Lower Devonian deposits (Tims & Chambers, 1984).

All plants in the Baragwanathia flora were herbaceous and probably occupied moist habitats because they undoubtedly required the presence of an aqueous environment for gamete exchange. The relatively complete preservation of many of the plant macrofossils and their frequent association with marine graptolites in the Victorian strata suggest that these plants were growing in coastal areas, perhaps in low herbfield communities along river flats and delta swamps (Tims, 1980). Various thalloid fossils are co-preserved with vascular plants of the Baragwanathia flora, but a lack of diagnostic features generally inhibits their assignation to particular algal groups.

The first trees: the Middle Devonian to Early Carboniferous lycophyte flora

Late Emsian or early Eifelian to Frasnian (late Early to early Late Devonian) plant assemblages record the first appearance of shrub- to tree-sized lycophyte floras in Australia and Antarctica which at that time were contiguous landmasses (Walkom, 1928; Gould, 1975; Truswell, 1991; McLoughlin & Long, 1994). The late Early and Middle Devonian floras were mostly dominated by herbaceous to shrub-sized lycophytes attributed to *Haplostigma*, *Leclercqia*, *Archaeosigillaria* and *Protolepidodendron*. Trimerophytes, early sphenophytes, and some plants of uncertain affinities (e.g. *Praeranunculus*) were probably also significant components of these floras. By the end of the Devonian (Famennian) some lycophytes (e.g. *Leptophloeum*) had attained the structure of tall trees (perhaps up to 20 m) and were colonists of lowland floodplains and coastal environments (Gould, 1975). As almost all elements in the Late Devonian floras probably relied on free water for transfer of their motile gametes, it is likely that large tracts of upland and drier habitats remained poorly- or un-vegetated.

Leptophloeum, the dominant element of the Late Devonian floras (Fig. 57), persisted into the Early Carboniferous and may have at least partly occupied strandline environments, based on the presence of log impressions often found associated with marine invertebrate fossils (Wyatt & Jell, 1967). Riverine transport to the marine environment and deposition as driftwood may also account for the co-preservation of these terrestrial and marine biotas. Apart from *Leptophloeum*, the Australian Late Devonian to Early Carboniferous floras contained a number of herbaceous, shrub-sized and arborescent lycophytes generally assigned to *Protolepidodendron*, *Ulodendron* and *Lepidodendron*. Species and genera of Devonian lycophytes are principally distinguished by differences in leaf morphology, shape and arrangement of leaf scars, and the arrangement of the vascular trace and parichnos scars on the plant axes. Relatively few detailed studies have been carried out on Australian floras of this age and most of the recognised genera were initially described from the Northern Hemisphere. Although Devonian floras do show a cosmopolitan aspect at higher taxonomic levels (Meyen, 1987), it is anticipated that future detailed studies of the Australian floras will show a greater degree of endemism at species level than is currently recognised.

The arborescent habit was mostly attained in lycophytes by the production of thick-walled periderm cells via secondary growth in the outer cortex. Some secondary growth was also achieved in the vascular tissue of arborescent lycophytes, but the thick cortical tissues appear to have been the chief means of physical support. This contrasts with arborescent progymnosperms and seed plants, which appeared at about the same time (progymnosperms in the Middle Devonian, 'seed-ferns' in the Late Devonian), and relied largely on secondary xylem tissue production for physical support. Ultimately, the use of secondary vascular tissue for support, together with improved vascular transport pathways, more elaborate leaf and branch modifications, and more sophisticated reproductive strategies, probably gave gymnosperms a competitive advantage in most terrestrial environments. Following Permian aridification in the Northern Hemisphere and glaciation in the Southern Hemisphere, the lycophytes appear never to have regained the stature of tall trees, although some pleuromeian lycophytes may have reached a few metres in height during the Triassic (Retallack, 1975).

A few zosterophyllophytes (*Barinophyton*) and rhyniophytes (*Taeniocrada*) appear to have persisted into the Australian Late Devonian floras but became increasingly overshadowed by new elements including sphenophytes (*Archaeocalamites*), ferns (*Adiantites*), and progymnosperms (?*Archaeopteris*) (Dun, 1897; White, 1986). Relatively diverse assemblages of cavate and acavate trilete spores preserved in Australian Devonian sequences also indicate the establishment of substantial lycophyte, fern, and sphenophyte communities during this period (Balme, 1962; Balme & Hassell, 1962; Playford, 1976; Grey, 1992).

Australian Middle and Late Devonian floras are generally considered to reflect warm conditions. Lycophyte axes from these floras typically do not show seasonal fluctuations in the size and arrangements of leaf scars, suggesting fairly uniform conditions throughout the year. Palaeomagnetic data indicate that Australia occupied low to middle southern latitudes in the Late Devonian (Embleton, 1984). Development of stromatoporoid- and coral-dominated reefs in north-western and eastern Australia, high marine invertebrate diversities, and development of red-beds and evaporites in central and north-eastern Australia are also evidence for the prevalence of warm climates (Wyatt & Jell, 1967, 1980; Quilty, 1984). Although terrestrial plant life was well-established by Late Devonian times, the only coals of this period are thin coaly laminae preserved in the Amadeus Basin of central Australia (Playford *et al.*, 1976).

While reefal limestones continued to accumulate in the north-west of the continent during the Early Carboniferous, Australia shifted towards higher latitudes and marine faunas from the south-east of the continent show a reduction in diversity probably corresponding to the onset of cool-water conditions. Terrestrial floras of the Early Carboniferous continued to be dominated by lycophytes, but evidence of more seasonal conditions is reflected in pronounced regular growth increments on the axes of these plants (Morris, 1980). Typical Late Devonian species were progressively replaced through the Early Carboniferous by a range of new lycophyte taxa, of which *Bumbudendron queenslandii* is one of the most prominent. Other Early Carboniferous plants included sphenophytes (*Archaeocalamites*), zygopterid ferns (*Austroclepsis*), and the first Australian seed-producing plants (*Nothorhacopteris*) of probable calamopityalean or callistophytalean affinities.

Carboniferous sedimentary sequences of North America and Europe incorporate thick coal deposits derived largely from lycophytes, sphenophytes, cordaitaleans, and medullosan seed-ferns. Extensive development of mire forests and the resulting large quantities of organic matter locked up in coal deposits probably induced marked changes in the proportions of O_2 and CO_2 in the atmosphere (Fig. 57) which in turn may have strongly influenced global climates. While some thin Carboniferous coals exist in eastern Australia (Rattigan, 1964), coal measure development was not nearly as pronounced as in the Northern Hemisphere. The dearth of Gondwanan coals probably relates to both unfavourable climates for development of persistent swamp communities (especially in the Late Carboniferous) and unfavourable geological settings for the accumulation of thick terrestrial sequences.

The first crisis: the Late Carboniferous to Early Permian Gondwanan glaciation

Between the Silurian and Permian periods Australia shifted from equatorial to near-polar latitudes (Embleton, 1984) (Fig. 57). This latitudinal shift was marked by dramatic climatic transformations and corresponding changes in the terrestrial flora. While Early Carboniferous floras contain lycophytes similar to those of the preceding Devonian period, Mid- to Late Carboniferous times saw a waning of the lycophyte floras and their replacement by low-diversity floras dominated by seed-ferns. Seed-ferns (also known as pteridosperms) were a polyphyletic group of plants which produced fern-like foliage but retained the megagametophyte stage upon the dominant sporophytic plant and encased their ovules in seeds. Seed-ferns also typically displayed some degree of secondary growth in their vascular tissues. Some seed-ferns (e.g. Calamopityales, Callistophytales) were probably derived from progymnosperm groups, some (e.g. Medullosales) shared affinities with cycadophytes, others (e.g. Glossopteridales) were probably related to conifers, cordaitaleans and ginkgophytes, while some Mesozoic representatives (e.g. Corystospermales, Bennettitales, Caytoniales) were possibly sister groups to the anthophytes (Crane, 1985; Meyen, 1987).

By the later part of the Early Carboniferous (late Visean or Namurian times), plants bearing pinnate *Nothorhacopteris* foliage dominated the Australian floras (Fig. 57). During the Late Carboniferous (Westphalian–Stephanian) *Nothorhacopteris* was replaced successively by *Fedekurtzia* and *Botrychiopsis* (Morris, 1980; Retallack, 1980) (Fig. 57). *Nothorhacopteris*, *Fedekurtzia*, *Botrychiopsis* and some less-common elements in the Late Carboniferous floras (e.g. *Cyclopteris* of Rigby, 1973) all share a basic pinnate or bipinnate frond morphology with gently divergent dichotomous venation in their pinnules, and are probably closely related. The botanical affinities of these plants are not yet clear, as convincing associated fructifications are yet to be found. Nevertheless, the Australian forms show strong similarities in their sterile foliage to Northern Hemisphere taxa attributed to both progymnosperms like the Archaeopteridales and seed-ferns like the Calamopityales and Callistophytales (Meyen, 1987). The *Nothorhacopteris-Fedekurtzia-Botrychiopsis* complex appears to have developed with the onset of cool climatic conditions in the mid-Carboniferous, reached its greatest abundance and diversity during the Late Carboniferous immediately prior to extensive Gondwanan glaciations, and persisted as minor elements (*Botrychiopsis* and *Bergiopteris*) within the succeeding *Glossopteris* flora until at least mid-Permian times.

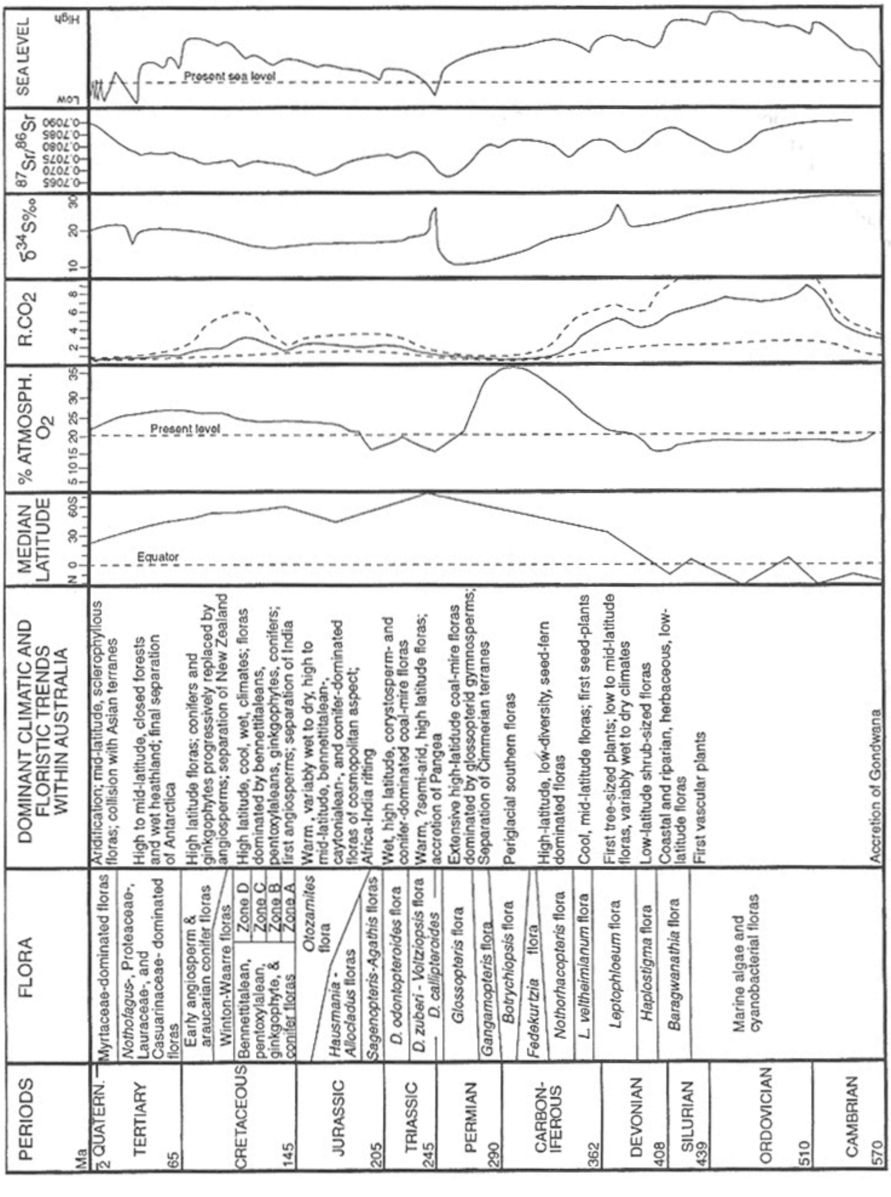

Figure 57. The succession of Australian terrestrial floras plotted against various geochemical, sea-level and latitudinal trends for the Phanerozoic. Time scales after Harland *et al*. (1990); Australia's median latitudinal position through time after Embleton (1984); best estimate of the percentage of O_2 in the atmosphere through time after Berner & Canfield (1989); best estimate of atmospheric CO_2 measured as a ratio of the mass of CO_2 at time *t* to that in the present atmosphere (dashed lines represent range of uncertainty) after Berner (1990); plot of mean $\delta^{34}S$ in sulphates through time after Odin *et al*. (1982); plot of strontium $^{87}Sr/^{86}Sr$ variation from marine carbonate, evaporite, and phosphate samples through time after Burke *et al*. (1982); broad-scale (mostly first- and second-order magnitude) phanerozoic sea-level fluctuation after Vail *et al*. (1977) and Hallam (1984).

Other plants occurring in the Late Carboniferous floras include calamitalean sphenophytes, lycophytes and rare ferns, but overall diversity within these floras was low. While low diversity may have been partly due to an unfavourable climatic setting, it may also be attributable to a dearth of systematic studies on these floras.

Lower Carboniferous palynofloras, like those of Upper Devonian sequences, comprise a diverse array of lycophyte, fern, sphenophyte and bryophyte spores (Playford, 1976, 1978; Powis, 1984; Playford & Satterthwait, 1985, 1986, 1988; Satterthwait & Playford, 1986). Although some spore-pollen taxa are long-ranging, the Upper Devonian to Lower Carboniferous palynofloras show progressive replacement of older taxa by new forms, potentially allowing detailed biostratigraphic zonation of the host strata (Playford, 1985). Mid-Carboniferous palynofloras continued to be dominated by trilete spores presumably derived from a range of lycophytes, sphenophytes, ferns and bryophytes, but monosaccate gymnosperm pollen also appears in the fossil record in low quantities around this time (Kemp *et al.*, 1977; Powis, 1984). Late Carboniferous (Stage 1) palynofloras contain a wealth of bilaterally and radially symmetrical monosaccate pollen, significant proportions of cryptogam spores, and very small amounts of bisaccate pollen (Balme, 1980). The rise in monosaccate abundance probably corresponds to global diversification of cordaitaleans and early conifers at this time. Although the macrofossil record for these groups in the Late Carboniferous and Early Permian of Australia is scanty, Argentinian sequences indicate that cordaites and conifers were well-established in Gondwana by this time (Archangelsky & Cúneo, 1987, 1991).

Post-glacial recovery: the Permian Glossopteris flora

The late Palaeozoic glaciation may have been diachronous across Gondwana (Crowell, 1995), but Australia appears to have been chiefly affected during the very late Carboniferous and Early Permian. During peak glacial times substantial ice caps probably covered many upland areas leaving evidence of glacial striae (Bourman & Alley, 1988), tillites (Crowell, 1971), and dropstones in marine sediments (Draper, 1983). Intervening lowland areas may have remained ice-free, and distinctive Gondwanan floristic elements (e.g. *Botrychiopsis*) persist from the Late Carboniferous through to the Early Permian. Major ice caps probably disappeared by mid-Permian times, and the post-glacial floras of Australia (and other major Gondwanan landmasses) were soon dominated by a newly evolved group of seed plants, the glossopterids (Fig. 57). Glossopterids produced distinctive, spatulate, reticulate-veined leaves and taeniate, bisaccate pollen, and both macrofossil and pollen remains of this group are first recorded at about the Carboniferous-Permian boundary (Rösler, 1978; Powis, 1984; Archangelsky *et al.*, 1987). Many Early Permian glossopterids possessed loosely meshed veins along the midline of their leaves; these forms are generally assigned to *Gangamopteris*. Leaves with medial veins strongly aggregated to form a prominent midrib are assigned to *Glossopteris* and occurred throughout the Permian but were dominant in the latter half of the Period. The differentiation of *Gangamopteris* and *Glossopteris* is arbitrary as both forms have been found attached to the same axes (Rigby, 1967).

Glossopterids hold a crucial place in both the economic development of Southern Hemisphere nations and in the understanding of past continental configurations. Permian coal deposits, composed predominantly of the remains of *Glossopteris* and allied plants, represent by far the dominant coal resources of the Southern Hemisphere. Measured and inferred Permian coal resources within Australia alone amount to well in excess of 120×10^9 tonnes (Maher *et al.*, 1995). The distribution of *Glossopteris* across the now widely separated landmasses was one of the key pieces of evidence used to support early propositions of continental drift and the former existence of a single Southern Hemisphere supercontinent, Gondwana (du Toit, 1937).

Glossopterids were primarily trees of lowland mire environments. Their distinctive root remains (*Vertebraria*) possess schizogenous cavities which were probably an adaptation for gas exchange in anoxic substrates (Neish *et al.*, 1993). Glossopterid leaves are often found in densely matted horizons suggesting a deciduous habit (Plumstead, 1969; Retallack, 1980). By the Late Permian the *Glossopteris* flora occupied a broad tract of the high southern latitudes (c. 40°–90°S, Fig. 58) and the deciduous habit may have been a response to strong seasonal photoperiod variation, and in some cases, several months of darkness. Fossil woods from the Permian of Australia and other Gondwanan continents invariably show prominent growth rings which probably also represented a response to a strongly seasonal climate.

The phylogenetic affinities of glossopterids have provoked more debate than perhaps any other group of plants. Much of the debate revolves around interpretation of the morphology and structural homologies of glossopterid ovulate fructifications. Two principal arguments currently prevail. The first suggests that the reproductive organs of glossopterids are homologous with the cupules of Mesozoic seed-ferns such as the Corystospermales and Caytoniales (Crane, 1985; Doyle & Donoghue, 1986). However, others have suggested that Mesozoic seed-fern cupules developed independently (Taylor *et al*., 1994), and that glossopterid fructifications may represent modified leaf and axillary shoot complexes more akin to cordaitaleans and early conifers (Schopf, 1976; McLoughlin, 1993a; McLoughlin & Drinnan, 1996).

Other plants represented in the Permian floras of Australia include cordaitaleans (*Noeggerathiopsis*), conifers (*Walkomiella*), osmundaceous ferns (*Neomariopteris*, *Dichotomopteris*, *Palaeosmunda*), numerous herbaceous sphenophytes (*Sphenophyllum*, *Trizygia*, *Phyllotheca*, *Lelstotheca*, *Raniganjia*, *Austroannularia*, *Gondwanophyton*), herbaceous lycophytes (*Cyclodendron*, *Selaginella*), cycadophytes (*Pseudoctenis*, *Pterophyllum*, *Dunedoonia*), rare ginkgophytes, and residual Palaeozoic seed-ferns (*Bergiopteris*). Despite the abundance of Permian plant fossils in Australia, the macroflora as a whole is of relatively low generic diversity. Greater diversity is apparent in the palynofloras, especially among pteridophytes (Foster, 1979; Gilby & Foster, 1988; Backhouse, 1993). It is possible that many pteridophytes occupied environments or had growth habits that did not favour preservation of their foliage in the fossil record, and distributional evidence of other plant groups (e.g. *Noeggerathiopsis* and *Walkomiella*) suggests that plant remains from upland areas were only rarely preserved along the cratonic flanks of the major sedimentary basins (for map of sedimentary basins see Fig. 32) or in small intracratonic basins (Retallack, 1980; McLoughlin, 1993b). Algal palynomorphs (presumably of freshwater origin) are also well-represented in Australian fluvial and paludal deposits (Balme & Segroves, 1966; Segroves, 1970; Foster, 1979; Backhouse, 1993) and occasionally formed thick accumulations of oil shale (Guy-Ohlsen, 1992).

Although by Permian times, most of the world's continental areas were united into a continuous landmass (Pangea), the strong equator-pole climatic gradients imposed by Gondwanan glaciation at the beginning of the period led to pronounced provincialism in the world's floras (Fig. 58). The *Glossopteris* flora represents the first expression of a truly unique Southern Hemisphere vegetation. Upper Carboniferous and Permian floras were also significant in that they saw the evolution of the conifers, ginkgophytes, peltasperms, cycads, and corystosperms, groups that were to become major components of the Mesozoic floras.

A second crisis: The Permian-Triassic extinction event

Close to the end of the Permian, coal measure sedimentation gave way to non-coaly fluvial deposits and red-beds in many parts of Australia and other Gondwanan landmasses. This sedimentological change closely corresponds to a sharp transition from glossopterid-dominated to moderate-diversity, corystosperm-, conifer-, and lycophyte-dominated floras. Palynological data suggest that the Permian-Triassic boundary (initially defined in European sedimentary sequences) is slightly higher in the succession than the major macrofloral and sedimentological transition in Australia (Foster, 1982).

The demise of glossopterids, and the disappearance or decline of medullosan seed-ferns, cordaitaleans, and gigantopterid gymnosperms in the Northern Hemisphere, together with the disappearance of numerous marine invertebrate taxa at or around the Permian-Triassic boundary, represent one of the major floristic extinction events in Earth history. Most recent studies dealing with the causes of extinction invoke broad-scale environmental changes (often prolonged marine regression at the end of the Permian followed by sharp

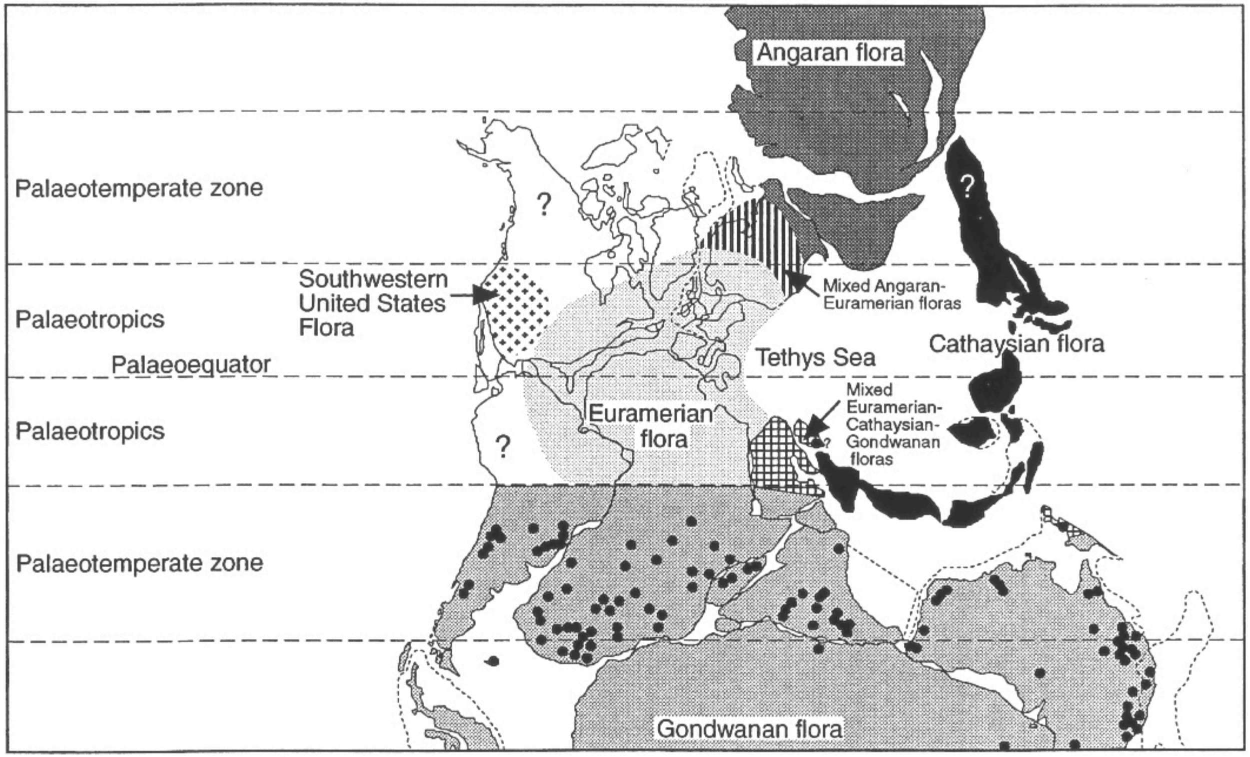

Figure 58. Reconstruction of Late Permian plate positions showing the distribution of the five major floristic provinces (modified from Chaloner & Creber, 1988). Gondwanan and Angaran floras are strongly correlated to southern and northern temperate to polar latitudes respectively, whereas the south-west United States, Euramerian, and Cathaysian floras are confined to the palaeotropics and occupied different humidity/aridity regimes or geographically isolated landmasses. Solid dots indicate the major sites of macrofossil assemblages of the *Glossopteris* flora.

transgression, and/or a shift towards more widespread arid conditions; Erwin, 1995). Clearly the end of the Permian was marked by major excursions from average sea-levels and ratios of stable isotopes in marine sediments (Erwin, 1994) (Fig. 57) reflecting rapid and pronounced environmental change. There is some evidence to suggest that the transition from floras of Palaeozoic to Mesozoic aspect was not globally synchronous, and that the transition in equatorial areas may have been more gradual than at higher latitudes (Meyen, 1987). Regardless of causes, the end-Permian extinctions probably provided opportunities for diversification of newly evolved groups like the Corystospermales, Caytoniales, cycadophytes, ginkgophytes and groups which had previously been more ecologically or geographically restricted (e.g. conifers and peltaspermalean seed-ferns).

The best Australian Early Triassic floras derive from the Sydney and Lorne Basins and the Nymboida Coal Measures. These floras are dominated by small-leafed voltzialean conifers (*Voltziopsis*), various *Dicroidium* (corystosperm) species, pleuromeian lycophytes (*Pleuromeia*, *Cyclostrobus*, *Cyclomeia*, *Cidarophyton*), osmundaceous (*Cladophlebis*), gleicheniacean (*Gleichenites*), dicksoniacean (*Todites*) and possibly marattiacean (*Rienitsia*) ferns, ginkgophytes (*Rhipidopsis*/*Sphenobaiera*), and possible pentoxylaleans or cycadophytes (*Taeniopteris*) (Walkom, 1925; Burges, 1935; Retallack, 1975, 1977; White, 1981; Chaloner & Turner, 1987; Holmes & Ash, 1979). Remains of these plant groups occur in varying assemblages through space and time and in association with differing palaeosol profiles and sedimentary deposits, leading Retallack (1977) to define three 'ecostratigraphic' assemblages for the Early Triassic. His 'Voltziopsetum' assemblage was dominated by conifer remains in association with humic and grey-brown podzolic soils and was interpreted as representing mainly coniferous forests developed on immature volcanic soils. The 'Dicroidietum zuberi' assemblage represented *Dicroidium*-dominated delta-top heaths and lagoon-margin, mire woodlands. The 'Pleuromeietum' assemblage, comprising an almost monospecific association of herbaceous to shrub-sized lycophytes, was interpreted to represent a coastal or saline, lagoon-margin flora. A marked increase in trilete, cavate spores (e.g. *Aratrisporites*, *Krauselisporites*, *Indotriradites*, *Densoisporites*, *Lundbladispora*) in Australian Early Triassic palynofloras is probably a result of rapid migration and diversification of opportunistic lycophyte species along the coasts of Pangea during Early Triassic transgression-regression cycles. Palynofloras from Early Triassic marine sequences in Australia are marked by low diversities but high abundances of simple spinose acritarchs which probably represent encystment stages of various unicellular algae (Balme, 1963; Balme & Helby, 1973).

Recovery and diversification in the Middle to Late Triassic: the *Dicroidium* flora

During the Middle and Late Triassic, climatic amelioration and local tectonism combined to favour a return to coal measure deposition in several isolated sedimentary basins of eastern and southern Australia. Generic diversity within Late Triassic coal measure floras (especially among the gymnosperm groups) is substantially greater than that in the glossopterid-dominated Permian coal floras. Late Triassic coal-mire floras were dominated by several species of corystosperm (*Dicroidium*) together with ginkgophytes (*Sphenobaiera*, *Ginkgoites*), cycadaleans (*Pseudoctenis*, *Nilssonia*), bennettitaleans (*Zamites*, *Anomozamites*), voltzialean and podocarp conifers (*Heidiphyllum*, *Rissikia*), peltasperms (*Lepidopteris*), dipteridacean (*Dictyophyllum*), marattiacean (*Ogmos*, *Marantoidea*), and osmundaceous (*Cladophlebis*, *Australosmunda*) ferns, sphenophytes (*Neocalamites*), bryophytes (see Webb & Holmes, 1982), and various seed-ferns of uncertain affinities (*Linguifolium, Yabiella*, *Pachydermophyllum, Dejerseya*, *Taeniopteris*).

As Middle and Late Triassic floras of eastern Australia become better understood, some compositional changes are now evident between floras of the various basins (Balme *et al.*, 1995) and between Australia and other Gondwanan regions (Anderson & Anderson, 1989). Triassic macrofloras of western and northern Australia are poorly known (White, 1961) but appear to contain at least some elements in common with eastern Australia. However, Late Triassic palynofloras from Western Australia include Tethyan (equatorial) elements that are absent in eastern Australia (Dolby & Balme, 1976). Tethyan-influenced palynofloras similar to the Western Australian (Onslow-type) assemblages are recorded from lower latitude portions of Gondwana flanking the Tethys Embayment, whereas eastern Australian (Ipswich-type) assemblages characterise higher Gondwanan palaeolatitudes (Foster *et al*., 1994).

Apart from regional variation, macrofloral assemblages also show compositional differences according to local habitats and depositional environments. In the Middle Triassic of the Sydney basin, plants bearing *Taeniopteris* foliage appear to have preferentially colonised levee banks of sluggish lowland rivers whereas *Dicroidium elongatum* occupied low-fertility, broad, sandy, floodplains. *Dicroidium odontopteroides*- and *Linguifolium*-dominated assemblages in the Late Triassic (Fig. 57) probably represent broad-leafed forests of coastal plain floodbasins. Assemblages dominated by *Heidiphyllum*, *Dicroidium stelznerianum*, *D. coriacea* and ginkgophytes, often occurring in coarse-grained sediments, probably represent accumulations of material derived from plants growing on well-drained sites (elevated levee banks and alluvial fans flanking upland regions). *Pachydermophyllum* associations from New Zealand (then a contiguous landmass with eastern Australia) are possibly derived from mangrove-like coastal communities (Retallack, 1977).

Many of the gymnospermous plants in the *Dicroidium* flora were probably deciduous, based on occurrences of their foliage in densely matted horizons, abscission of whole leaves, and the expanded bases and well-defined abscission zones on some leaves (Anderson & Anderson, 1989). The transition, in many areas, from red-beds in the Early and Middle Triassic to coal measures in the Late Triassic, probably reflects a shift towards generally wetter conditions. Thick cuticles and strong stomatal protection on some plants of the *Dicroidium* flora may represent adaptations to combat water stress (Cantrill *et al*., 1995). On the other hand, wet and relatively warm conditions are suggested by the presence of dipteridacean and marattiacean ferns, although it is difficult to judge whether Triassic representatives of these groups favoured the same climatic conditions as their extant relatives. Thick cuticles and stomatal protection on some of these plants may have been a response to growth on infertile or relatively arid substrates (Retallack, 1977).

Dinoflagellates (Division Pyrrophyta) underwent a major phase of diversification in marine environments during the Late Triassic and retained high diversities throughout the remainder of the Mesozoic and Cainozoic. It is likely that many of the Palaeozoic and Triassic acritarchs from marine sediments represent encystment stages of dinoflagellates or their close relatives. Coccolithophores (Division Chrysophyta; Class Coccolithophyceae) also first appeared in the Late Triassic and underwent a major radiation in the Early Jurassic. Like the dinoflagellates, they appear to have reached peak diversity in the extensive shallow seas of the Late Cretaceous, and remain important components of the modern oceanic phytoplankton.

Masters of the Jurassic: bennettitaleans, pentoxylaleans, and conifers

Early Jurassic floras are not well-represented in Australia; assemblages are known only from Queensland and New South Wales. Several notable Late Triassic genera (e.g. *Dicroidium*, *Linguifolium*, *Dejerseya*, *Yabiella* and *Heidiphyllum*) are absent from the Early Jurassic floras, indicating a major extinction event coinciding with that experienced globally by terrestrial vertebrate and marine invertebrate faunas (Stanley, 1987). Dinosaurs, which had first appeared during the Triassic, came to dominate the large terrestrial herbivore and carnivore niches following the end-Triassic extinctions and remained the dominant terrestrial vertebrates for the remainder of the Mesozoic. Accompanying the faunal turnovers, new plant taxa including representatives of the Bennettitales (*Otozamites*), Caytoniales (*Sagenopteris*), and cheirolepidacean conifers (known only from their abundant, dispersed, *Classopollis* pollen) take the place of some of the Late Triassic gymnosperms, although total diversity appears to have fallen (Balme *et al*., 1995). Other elements in the Early Jurassic floras include marattiacean (*Phlebopteris*), osmundacean (*Cladophlebis*), dicksoniacean (*Todites*) and dipteridacean (*Dictyophyllum*) ferns, equisetaleans (*Equisetum*), lycophytes (*Selaginella*, *Isoetites*), cycadaleans (*Nilssonia*), podocarp and araucariacean conifers (*Rissikia*/*Elatocladus*, *Allocladus*, *Agathis*), pentoxylaleans (*Taeniopteris*), and some seed-ferns of uncertain alliance (*Pachypteris*, *Thinnfeldia*).

Australia occupied middle to high (c. 35°–65°) southern latitudes in the Jurassic, probably resulting in a considerable north-west to south-east climatic gradient across the continent. The palaeoclimatic signatures of many of the Jurassic plant groups are unclear as they were either widely dispersed in the Jurassic and/or have few or no close extant relatives. Although some endemic or strongly Gondwanan elements are evident in the Early Jurassic floras (pentoxylaleans, araucariaceans), the floras have a more cosmopolitan aspect than those of the Permian and Triassic, and this may imply both easy migration pathways through a united Pangea and more equable climates globally. Although good palaeoclimatic indicators are often lacking, stable isotope studies, the absence of red-beds, presence of local coal deposits and the lack of evidence for glaciation suggests that conditions were generally warm and, on the whole, relatively humid during the Australian Jurassic. However, it must be emphasised that much of the macrofossil data for this period derives from eastern Australia and some palynological studies from Western Australia have suggested the possibility of arid conditions in that region, at least for the Early Jurassic (Filatoff, 1975).

Middle Jurassic floras are best known from the Walloon Coal Measures and their equivalents in the Clarence-Moreton and Surat Basins of southern Queensland and northern New South Wales. These floras share many taxa with Early Jurassic assemblages but lack caytonialeans (*Sagenopteris*). The Walloon floras show considerable compositional differences between assemblages derived from coal seams and carbonaceous floodbasin deposits underlying coals, and those derived from interseam channel, levee and crevasse deposits. The former are rich in equisetaleans (*Equisetum*), osmundaceous (*Cladophlebis*, *Osmundacaulis*, *Millerocaulis*, *Grammatocaulis*, *Ashicaulis*) and dipteridacean (*Hausmannia*) ferns, and pentoxylaleans (*Pentoxylon*, *Taeniopteris*), whereas the latter are generally dominated by bennettitaleans (*Otozamites*, *Ptilophyllum*) and podocarp and araucarian conifers (*Mataia*, *Pagiophyllum, Araucaria, Allocladus*, *Bellarinea*). Several studies of the Walloon floras have noted the conspicuous absence of ginkgophytes in contrast to their prominent representation in contemporaneous floras from other parts of the world (Gould, 1980; McLoughlin & Drinnan, 1995). Other elements in the Middle Jurassic floras include dicksoniacean ferns (*Coniopteris*), ferns of uncertain affinities (*Sphenopteris*) and gymnosperms of uncertain alliance (*Pachypteris*, *Palissya*). *Palissya* has occasionally been considered to have affinities with *Elatocladus*-type foliage and is therefore often regarded as coniferous, but no direct connection between cone and foliage has yet been found and the structure of *Palissya* is unlike that of other conifer reproductive organs (Parris *et al*., 1995). Late Jurassic floras are very poorly known but appear to incorporate most of the same elements (at generic level) as Middle Jurassic floras and are especially well-represented by osmundaceous (*Cladophlebis*, *Osmundacaulis*, *Millerocaulis*, *Ashicaulis*), cyatheacean (*Oguracaulis*, *Cibotium*) and dicksoniacean (*Coniopteris*) ferns, bennettitaleans (*Otozamites*, *Ptilophyllum*) and conifers (Gould, 1975, 1978; Tidwell *et al*., 1987, 1991).

Diatoms (Phylum Chrysophyta; Class Bacillariophyceae) first appear in Late Jurassic marine sediments and the group consistently diversified throughout the remainder of the Mesozoic and Cainozoic. They presently represent a major component of the marine phytoplankton and have successfully invaded freshwater and some terrestrial habitats. As diatom species commonly have distinct temperature, salinity, acidity, oxygen, and mineral nutrient requirements, their fossil distribution has been of great value for palaeoenvironmental and palaeoclimatic studies (Brasier, 1980).

The Middle and Late Jurassic floras of eastern Australia occurred at palaeolatitudes of around 55°–65°S (Embleton, 1984; Veevers *et al*., 1991). These floras contain some apparently deciduous elements (*Taeniopteris*), and both floral diversity and oxygen isotope data suggest that humid mesothermal to microthermal climates prevailed (Gould, 1980). A Middle to Late Jurassic flora from Western Australia, which developed in palaeolatitudes of around 35°–40°S, appears to have a higher proportion of araucarian conifers and bennettitaleans (Arber, 1910; Walkom, 1921; McLoughlin & Hill, 1996) and may represent

(1) a flora botanically more akin to Early Cretaceous assemblages,

(2) an assemblage derived from a generally drier or warmer climate, or

(3) an assemblage derived from upland plant communities.

The cosmopolitan aspect of the Australian flora evident in the Early Jurassic appears to have persisted to some extent until the end of the Jurassic although some distinctive Gondwanan elements are represented throughout the period. The Late Jurassic saw the initiation of rifting and sea-floor spreading on the north-western margin of Australia (Veevers *et al*., 1991) and between Africa and India. Rifting continued along the western, southern, and eastern margins of Australia through the Cretaceous and early Tertiary and had profound implications for the geographic isolation of the continent and the development of a unique Australian biota.

The Cretaceous flora

Most of the modern Australia flora had its genesis in the long span of time called the Cretaceous Period. Recently, the three-element invasion hypothesis that was initially advocated by Hooker (1860) (but see Crisp *et al*., this volume) to explain the present-day Australian flora has been rejected (Barlow, 1981; Webb *et al*., 1986; Dettmann, 1994) and replaced by a more complex set of hypotheses indicating autochthonous differentiation from an ancient Gondwanan flora during the Late Cretaceous and Early Tertiary (Webb *et al*., 1986), and possibly a Late Cretaceous-Early Tertiary phase of floristic exchange between Australia and regions to the north, with dispersal occurring in both directions (Truswell *et al*., 1987; Hill, 1992; Hill & Dettmann, 1996). Evidence countering invasion from the north during the Late Cretaceous has accrued (Dettmann & Thomson, 1987; Dettmann & Jarzen, 1988, 1990; Dettmann, 1989; Jarzen & Dettmann, 1989; Dettmann *et al*., 1990) and further testing of this hypothesis requires detailed palynological records from the Late Cretaceous of northern Australasia. From patterns of pollen introductions in separate regions of the southern Gondwana assembly it is clear that many elements of the Australian Cretaceous flora either evolved within the Austro-Antarctic region or entered Australia using an Antarctic route (Dettmann, 1981, 1989; Dettmann & Jarzen, 1990). Clearly, the Cretaceous was a time of enormous significance to the evolution of the current Australian flora.

Throughout the Cretaceous, Australia remained connected to Antarctica and was situated at very high latitudes (especially the southernmost parts, Fig. 59). Given the lack of the extreme polar cold that is experienced today, this led to growth conditions that have no modern analogue, i.e. extreme fluctuations in annual photoperiod coupled with a relatively benign climate. There were probably also atmospheric CO_2 levels well above those within human experience (Barron & Washington, 1985), and disturbance patterns associated with the rifting of Gondwana that were well beyond any experienced in Australia in more recent times. Some of the direct and indirect consequences of these physical conditions are considered prior to an examination of the fossil record.

High latitude areas as regions of evolutionary novelty

High latitude areas have been suggested as important sources of evolutionary novelties, a hypothesis that has its origins in the work of Jablonski *et al*. (1983), who noted the preferential generation of evolutionary novelties in nearshore, as opposed to offshore, communities in the fossil record. They proposed two reasons for this:

- Evolutionary novelties are equally likely in all speciation events, but the greater extinction resistance in nearshore species permits novelties to persist long enough to diversify (i.e. nearshore innovations have a higher probability of persisting long enough to diversify, and there is also an increase in the total number of speciation events in a clade over its lifetime).
- The ecological constraints of certain types of environments enhance the likelihood of large evolutionary jumps during speciation events.

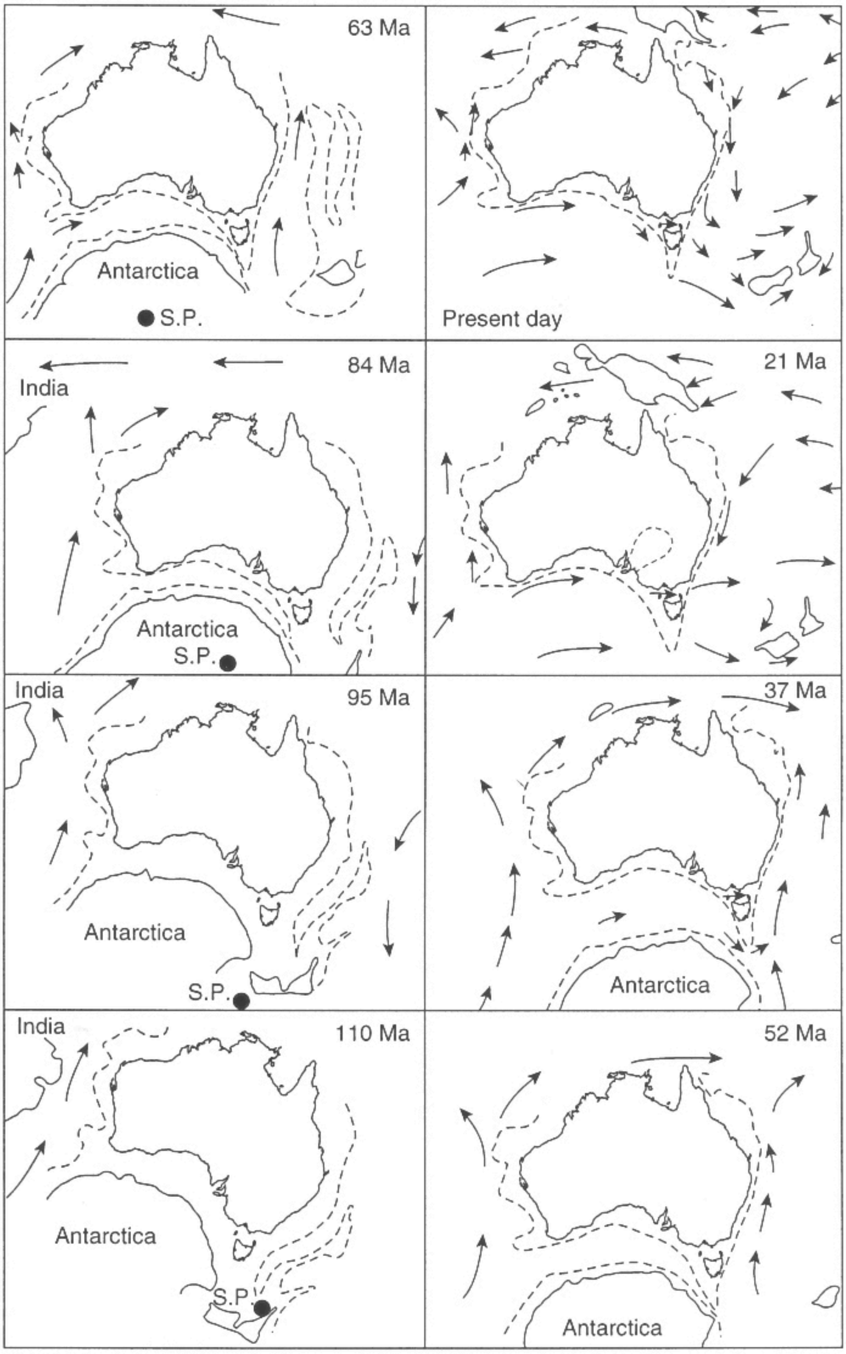

Figure 59. Variation in oceanic current patterns through the Cretaceous and Cenozoic of Australia. S.P. = South Pole. Arrows indicate positions of surface currents. Present continental outlines are shown as solid lines and bear little relation to positions of past coastlines. Broken lines represent the continent-ocean boundaries. Modified from Quilty (1994).

Lewin (1983) took the important step of equating the nearshore environment of Jablonski *et al.* (1983) with a high latitude terrestrial habitat. High latitude habitats are generally hazardous places to live compared with the relatively stable low latitude habitats. Consequently, low latitude species are able to thrive as small, geographically restricted populations, leading to characteristically high species diversity in the tropics, whereas high latitude regions are composed of large, widely distributed populations. Lewin (1983) proposed that peripherally isolated groups drawn from such a large, widespread population may undergo 'minigenetic revolutions', which could shift developmental patterns sufficiently to produce truly novel forms (a phenomenon called 'genetic transilience' by Templeton (in Lewin, 1983)). It is not yet clear whether either or both of these options operate.

Hickey *et al.* (1983) provided strong evidence to support the hypothesis that the terrestrial Arctic biota of the latest Cretaceous and Palaeogene was profoundly out of phase with that of more southerly latitudes, with many taxa appearing first at the higher latitudes. They concluded that during much of the Phanerozoic the currently inhospitable Arctic region may have served as the birthplace for important biotic innovations and for major groups that later radiated to lower latitudes.

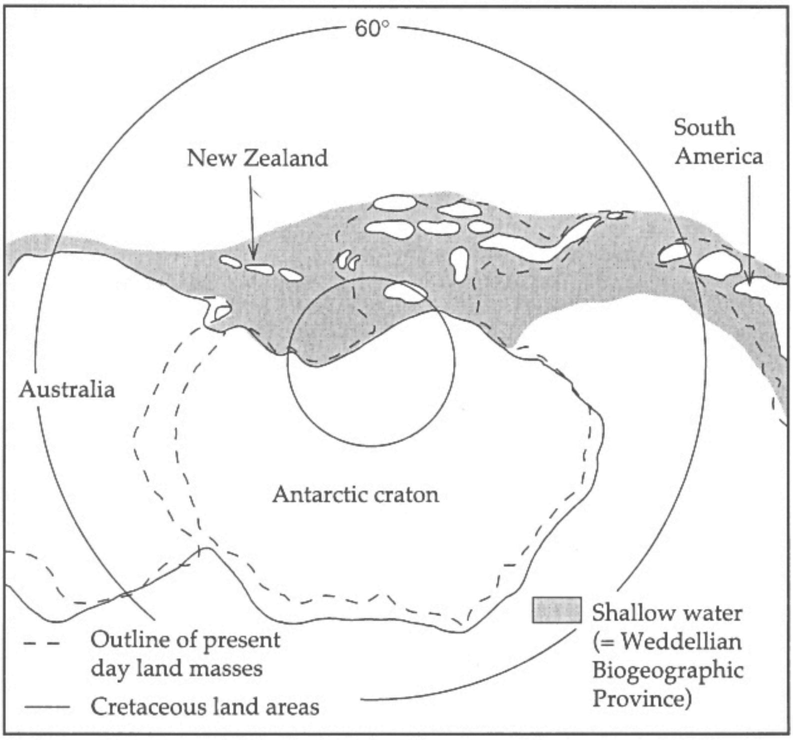
60°
South America
New Zealand
Australia
Antarctic craton
Shallow water (= Weddellian Biogeographic Province)
Outline of present day land masses
Cretaceous land areas

Figure 60. Reconstruction of the Weddellian Biogeographic Province (stippled area) during the Late Cretaceous and Paleogene. Modified from Case (1988) who considered that the stippled area should represent a continuous coastal environment bordered by shallow seas.

Zinmeister & Feldman (1984) provided data supporting a similar high latitude heterochroneity for Southern Hemisphere marine faunas during the Cretaceous, and Case (1988, 1989) extended the Weddellian Zoogeographic Province (Fig. 60) to a 'biogeographic province' to take account of this for the terrestrial biota. Case hypothesised that this province was a centre of origin and diversification for many taxa, particularly marsupials and species of *Nothofagus*, during the Late Cretaceous and Palaeogene. Askin (1989) concluded that although much of the Antarctic Cretaceous-Cainozoic endemic flora remained isolated because of geographical, climatic or biological barriers, many plants spread northwards, introducing dominant taxa to later mid-latitude floras, and other taxa to mid- to low-latitude floras. As will be seen in the following discussion of the fossil record, it is now clear that the Weddellian Biogeographic Province was the source of much of the Australian flora, and there is strong evidence for a Southern Hemisphere equivalent of the heterochroneity reported by Hickey *et al*. (1983) for high northern latitudes (Askin, 1989; Dettmann, 1989; Hill & Scriven, 1995).

The role of disturbance in Gondwana and early angiosperm migration

Angiosperms evolved in the northern Gondwana/southern Laurasia area during the Early Cretaceous and radiated world-wide (Drinnan & Crane, 1990; Dettmann, 1992). Retallack & Dilcher (1981) hypothesised that early angiosperms had generalised pollination and dispersal strategies. This made them ideal for long-range dispersal by pioneering the fresh sedimentary surfaces of coastal deltas, lagoons, and tidal flats. As the extent of marine transgression and regression increased in North America during the Early Cretaceous, these pioneering early angiosperms or angiosperm ancestors dispersed along coastlines out of the rift valley of West Gondwana (between Africa and South America). More recent research has confirmed an early successional role for early angiosperms (e.g. Wing & Tiffney, 1987), and this has been used in a novel but as yet untested way to account for the early radiation of angiosperms in a dinosaur-dominated world (Bakker, 1988).

Angiosperms spread generally into Gondwana during latest Barremian–Aptian times (Dettmann, 1989), and those lineages that were established in southern Gondwana by the close of the Cretaceous formed the foundation from which present-day austral floras developed (Dettmann, 1992). Dettmann (1989) noted that rift valley systems at high southern latitudes acted as migrational pathways for early angiosperms, perhaps because of the high disturbance level in these environments and the colonising nature of these angiosperms.

Some of the prominent taxa in the early high southern latitude flora still exist elsewhere today, and their ecology is well-understood. A good example is *Nothofagus*, which has been studied extensively across its range. For example, Veblen *et al*. (1977, 1980) noted that *Nothofagus* in South America does not usually regenerate continuously at low altitudes, especially at lower latitudes, where climatic conditions favour more complex forests and *Nothofagus* seedlings cannot establish. In these environments, *Nothofagus* relies on catastrophic disturbance, a relatively common phenomenon in the highly unstable Andes mountain chain, to provide a fresh, cleared substrate which is readily colonised by seedlings. This regeneration behaviour is probably very similar to that which occurred early in the history of the genus, when it occupied either dense forests on unstable sites, and was unable to regenerate in the absence of disturbance, or occurred in more sparse forest on less equable sites where its seedlings could survive in the understorey. Hill (1987, 1992) hypothesised that the large reduction in *Nothofagus* diversity at high latitudes today, especially away from the Andes, may be due to the relative stability of the modern landscape, which, coupled with the density of the forest cover, does not provide a suitable environment for the continued presence of many *Nothofagus* species.

Thus it is highly probable that unstable habitats at high southern latitudes during the Cretaceous-Palaeogene provided both a pathway for the migration of early angiosperms and the potential for peripheral isolation of populations of widespread species. This may have been a critical factor for evolution in the region (Hill & Scriven, 1995).

Plant growth at high southern latitudes

One obvious question about forest growth at high southern latitudes in the Cretaceous-Palaeogene is: how did plants grow and what form did the communities take in such an unusual photoperiod? It is a real limitation of the fossil record in general that behavioural traits such as dormancy rarely leave a clear imprint (Truswell, 1991). However, information on physiological adaptations to life at high latitudes can be obtained from an examination of fossil wood and leaf form. Cretaceous gymnospermous wood from palaeolatitudes probably higher than 70°S, shows a consistent pattern of growth, with increments, probably annual in origin, clearly delineated, and indicating a pronounced seasonal influence (Jefferson, 1982). The amount of wood added annually was usually large, even when compared with modern low-latitude trees, but there is considerable variation in ring widths from year to year, suggesting that the trees were highly sensitive to environmental fluctuations (Truswell, 1991). A fossil forest at one early Cretaceous site had trees spaced 3–5 m apart and the tallest preserved trunk height is 7 m (Jefferson, 1982). Hill (1994a) used these data to explain the reduction in wind pollination in understorey plants during the very early Palaeogene in southern Australia. With the sun at a low angle in the sky during summer and tracking an almost circular path around the horizon during the day, he concluded that it was likely that the forest structure was quite different to that observed in heavily forested regions of Australia today. As has been postulated for the Late Cretaceous (Specht *et al*., 1992), relatively widely spaced conical trees probably dominated, and thus wind pollination was a viable strategy for understorey plants below the open canopy. As Australia moved into lower latitudes and the sun angle increased, a closed forest structure developed as the most efficient way of utilising incoming solar radiation. This may have been critical for the loss of wind pollination as a viable strategy in the associated understorey plants.

Leaf physiognomy is a well-established palaeobotanical data source, but its application to high latitude macrofloras is controversial. The extremely unusual light conditions present in southern Australia and Antarctica probably had a profound effect on leaf structure in the forests of the Cretaceous-Palaeogene. For example, Wells & Hill (1993) proposed that leaves in Palaeogene forests of southern Australia may have hung vertically to increase light capture, because the sun was continually at a low angle. If this was so, then the same would have applied in the Cretaceous, and such a strategy may well have led to the evolution of unusual leaf sizes and shapes which are not amenable to comparison with data gathered from extant forests (Hill & Scriven, 1995).

Another approach to predicting palaeoclimate is to examine in detail the morphology of fossil leaves. This has been done for the podocarp genera *Acmopyle* and *Dacrycarpus* in the Palaeogene of south-eastern Australia (Hill & Carpenter, 1991; Hill, 1994a). Here leaf size and stomatal distribution were found to be related to climate (see below), but this approach has not yet been applied to Cretaceous fossils.

The presence of a relatively dense plant cover, including large and rapidly growing trees, in regions poleward of the Antarctic circle has long appeared enigmatic, given that today growth at high latitudes is viewed as being constrained by characteristic day-length patterns, and by the temperatures associated with a regime of long rigorous winters and short cool summers (Truswell, 1991). Truswell pointed out that the problems raised by the fossil record include:

- How plants coped with the conditions imposed by the polar night;
- How the growth of substantial forests could have been sustained at latitudes where no light, and as a consequence, little heat energy, was available for several months of the year, and where growing seasons were as short as two to three months.

Several explanations have been published to account for inconsistencies between the growth forms demonstrated by the fossil record, and the high latitude at which the past floras apparently grew.

Some of these explanations can be disregarded. Among these are the view that Antarctica only came to be in high latitudes relatively recently, a hypothesis which has been refuted by palaeomagnetic data on pole positions and the constraints imposed by seafloor spreading data, which indicate that the Antarctic continent has occupied a near-polar position for much of the Phanerozoic (Smith *et al.*, 1981; Truswell, 1991). Similarly, changes in the angle of obliquity of the Earth's spin axis have occasionally been invoked (e.g. Wolfe, 1978, 1980; Douglas & Williams, 1982; Jefferson, 1982, 1983) to explain the presence of diverse vegetation at high latitudes. Creber & Chaloner (1985) examined and rejected all models proposed to account for changes in the angle of the Earth's axis.

It is far simpler to examine the most likely option, that plants can thrive in high latitudes provided the climate is not too hostile. The idea that light energy at high latitudes, at present values of axial obliquity, was sufficient to maintain forest growth in the past, provided that temperatures were higher, particularly in winter, was supported in arguments synthesised by Axelrod (1984), although these were not based on quantitative experimentation. More recently, physiological experiments on living plants have provided even more compelling support. Read & Francis (1992) examined the tolerance of some woody species to prolonged dark periods, particularly in warm and dark versus cold and dark conditions, and attempted to identify common characteristics among these species which may have influenced survival.

Their results indicated that at least some woody plant species native to the Southern Hemisphere can survive 10 weeks of continual darkness. Notably, survival across these species was higher under cold (at least to 4°C) dark conditions than under warm dark conditions. Species varied in their capacity to tolerate long dark periods, but the physiological determinants of this differential tolerance are as yet uncertain. However, from their limited data it appears that the deciduous habit may be advantageous, and in evergreen plants a low dark respiration rate, and perhaps other features of their light saturation curves, are potentially important. The latter characteristics may, however, decline in importance as the temperature during the dark period declines. It is apparent from the results of Read & Francis (1992) that some species experienced little stress under long dark periods, without critical loss of stored starch, and without any detectable irreversible effects on the leaf photosynthetic apparatus.

Lower winter temperatures of the more seasonal, inland continental climate at high southern latitudes in the Cretaceous-Palaeogene would have reduced respirational loss and would have been more suitable for many plant species than the milder climate at coastal margins. In addition, cloudiness, which is higher at the coastal margins than the interior of the current Antarctic landmass, has a considerable effect on sunshine hours. Interspecific differences in, for example, photosynthetic responses to light and temperature, may therefore have led to differential occurrence of species, habit (e.g. deciduous versus evergreen) and vegetation type, with respect to coastal versus inland regions of southern Australia and Antarctica.

These results also led Read & Francis (1992) to question the value of deciduousness in these high latitude floras. The apparent infrequency of deciduousness in Southern Hemisphere Cretaceous and Cainozoic fossil floras compared with those of the Northern Hemisphere may reflect differences in either winter or growing season conditions, but the recognition of deciduousness in the fossil record is often controversial, and data are required on the extent of this strategy as inferred from the fossil record (Hill & Scriven, 1995).

Creber & Chaloner (1984) reinforced the view that ambient temperature, rather than the available light, is the factor limiting tree growth in high latitudes today. They cited data which demonstrate that the amount of light energy available at latitudes within the Antarctic circle may not be significantly less than that at temperate latitudes. It is clearly adequate for tree growth, provided that the low-angle solar rays can be intercepted without excessive interference caused by mutual shading. The spacing and shape of trees are obviously crucial. Creber & Chaloner noted that the density of trees in Jefferson's (1982) Early Cretaceous forest, at one tree per 17 m^2, or 588 trees per hectare, is sparse enough for them to have intercepted sufficient illumination to produce the observed growth, provided the trees were tall and conical in shape, with a vertical canopy.

Creber & Chaloner (1985) also suggested that enhanced atmospheric CO_2 levels may have been influential in producing the high annual increments of growth observed in Cretaceous trees. The overall effect of the high predicted levels of CO_2 in the Cretaceous on plant growth is difficult to quantify, since experiments carried out on living plants are examining the instantaneous effects of large changes in CO_2 concentration on plants which have evolved to a particular ambient level. When plants had evolved to accommodate higher levels (as in the Cretaceous) the result may have been even greater (Hill & Scriven, 1995).

The flora prior to angiosperm invasion (early Berriasian–Barremian)

In the earliest Cretaceous, Australia, Antarctica, New Zealand, the Lord Howe Rise, the Queensland Plateau, and greater India were conjoined as part of the Gondwana landmass, with Australia situated between latitudes of 50° and 80°S (Dettmann, 1994). Seafloor spreading at this time progressed southward and eastward around the Australian continent during the earliest Cretaceous (BMR Palaeogeographic Group, 1990; Veevers *et al.*, 1991).

The Early Cretaceous floras resembled those of the Middle and Late Jurassic, but by the end of the period many of the taxa had become extinct and the angiosperms had come into prominence (Douglas, 1994). Sediments preserved in over 20 major depositional basins in Australia contain a significant record of this vegetation, but the record is both spatially and temporally patchy.

The oldest macrofloras, assigned to Zone A by Douglas (1969) in the best researched area, the Otway Basin of south-eastern Australia, are little known because of the few known deposits and their poor preservation in the older subsurface part of the succession (Douglas, 1994). The best known element is the bennettitaleans, represented as three leaf compression taxa that are considered to have been understorey components, reminiscent of classical Jurassic (e.g. Yorkshire) floras (Douglas, 1994). Silcrete layers in the Algebuckina Sandstone (Eromanga Basin) of central Australia (Hopgood, 1987) suggest a canopy of conifers (*Brachyphyllum*) with an understorey of pteridosperms, cycads, bennettitaleans, and cryptogams. Terrestrial ferns, an *Isoetes*-like fossil, and two common leaves (*Rienitsia variabilis* and *Taeniopteris spatulata* (?Pentoxylales)) occur here, and they have more affinities with the later (Zone B of Douglas, 1969) floras of the south-east (Douglas, 1994). Preliminary work on collections from the Surat Basin in Queensland (Cantrill & Webb, 1987) indicates a conifer and *Ginkgo digitata* canopy over ferns, an *Equisetum*-like sphenopsid, and pteridosperms. Rozefelds (1988) reported the corystosperm *Pachypteris* and cryptogams from the Laura Basin in northern Queensland. Cretaceous macrofloras from a variety of localities in Western Australia incorporate a range of lycophytes, ferns, pteridosperms, bennettitaleans and conifers, and most closely resemble those from the Algebuckina Sandstone (McLoughlin, 1996) or possibly the Zone B floras of the Otway Basin.

The relationship of several orders of pteridosperms (e.g. Peltaspermales, Corystospermales, Caytoniales) is not clearly defined (Harland *et al.*, 1967) and thus it is difficult to reconstruct their ecological niches as well as their phylogenetic position (Douglas, 1994). Among the bennettitaleans *Ptilophyllum boolensis*, which has fine pinnate leaves, has been interpreted as a semi-prostrate ground cover, or climber (Douglas, 1994). Bennettitaleans are not preserved as the silicified trunks which occur in many overseas localities, and the only indication of a main axis is stem fragments bearing two or three pinnae (Douglas, 1994). Apart from a few rare occurrences in parts of the section of disputed age, bennettitalean macrofossils have not been found in younger Australian assemblages.

In the Zone B floras of the Otway Basin (Douglas, 1969), leaf fragments (*Ctenis? coronata*) provide one of the very few macrofossil records of the Cycadales in the Cretaceous of south-eastern Australia, where the order is not otherwise recorded until the Palaeogene (Hill, 1978, 1980; Douglas, 1994; Hill & Pole, 1994). *Ginkgo australis*, a key zone macrofossil in younger beds of the south-east of the continent, appears for the first time in the fossil record, with *Taeniopteris* and *Phyllopteroides*, in the Surat Basin. The Stanwell Coal Measures flora (Queensland) also contains these two latter genera (Cantrill & Webb, 1987).

The earliest Cretaceous palynological data indicate that araucarians and podocarps were important elements in the Australian vegetation (Dettmann, 1994). Abundant pollen of these austral conifers, including the *Araucaria*/*Agathis*-, *Podocarpus*-, and *Microcachrys*-types (Fig. 61), are associated with frequent pollen indicative of pteridosperms and/or bennettitaleans, and cycadophytes and/or ginkgophytes (Dettmann, 1994), and this is

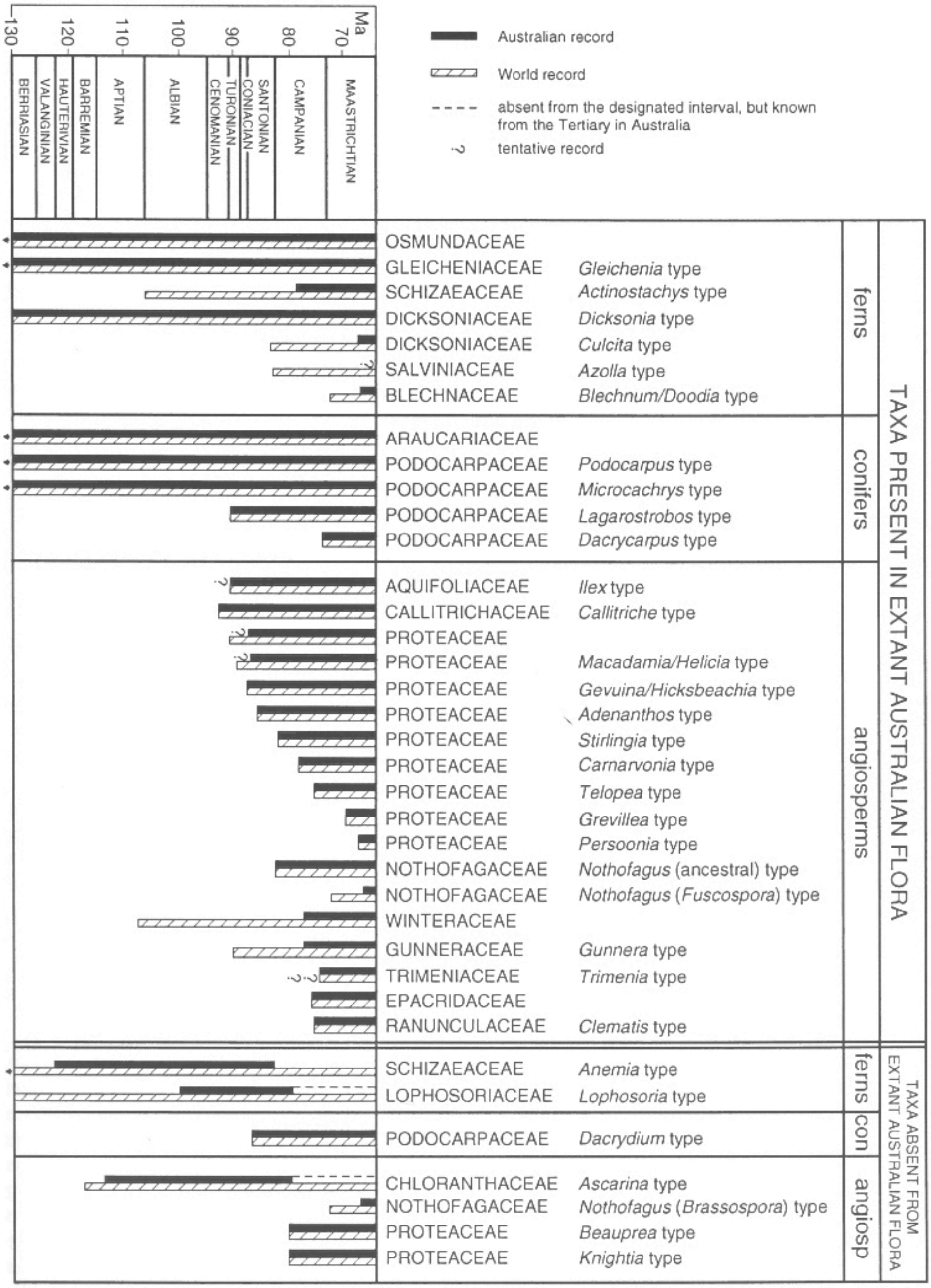

Figure 61. Time ranges of selected taxa represented in the Cretaceous vegetation of Australia. Time ranges on a world basis are shown for each taxon. (After Dettmann, 1994). (con. = conifer).

mirrored by a macrofossil record of related taxa (see above). *Classopollis* and *Corollina*, indicators of cheirolepidacean conifers, occur in low frequencies in fluvial/lacustrine sediments, but are usually common in marginal marine sediments. Araucarian/podocarp forests probably surrounded river and lake systems, but in coastal regions the forests gave way to cheirolepidacean woodlands (Dettmann, 1994). Spores and/or macrofossils of ferns (including meagre evidence of the aquatic Marsileales), lycopods, isoetaleans, equisetaleans and bryophytes are both abundant and diverse in sediments that accumulated in coastal and inland regions (Dettmann, 1994; Douglas, 1994).

The floral evidence suggests some regionalism among overstorey and understorey communities in the earliest Cretaceous Australian vegetation. The broad riverine area of the Eromanga/Surat Basins supported a more diverse fern, lycopod and moss flora than the narrow depressions of the Otway/Gippsland Basins in the southern rift valleys, which appear to have been more uniformly forested (Dettmann, 1994). In the Perth Basin in Western Australia, diverse assemblages of ferns were represented, including several taxa that are unknown from the south-east prior to the Barremian (Dettmann, 1986a; Helby *et al*., 1987; Dettmann *et al*., 1992). Migration of these taxa from the west may have been triggered by tectonic/volcanic disturbances that heralded rifting of India from south-western Australia and widening of the southern rift valley (Dettmann, 1994).

A major rise in relative sea level during late Valanginian to early Barremian times led to marked changes in depositional patterns. India broke away from Australia accompanied by widespread faulting and extrusion of basalts, and the rift between Australia and Antarctica slowly widened, but drainage patterns changed little.

Fossil floras from this time indicate a response of the vegetation to these environmental disturbances. There was an increased representation of the Podocarpaceae, possibly in response to increased precipitation (Dettmann, 1994; Douglas, 1994). However, cheirolepidacean woodlands were well-developed in coastal regions of south-western Australia (Backhouse, 1988).

Earlier concepts of a uniform flora over Australia during earliest Cretaceous times have been revised. Distinct community associations recorded from the disparate depositional areas indicate a regionalised vegetation that reflects latitudinal control as well as habitat differences related to topographic and substrate variations (Dettmann 1986a, 1986b, 1994; Dettmann *et al*., 1992; Douglas, 1994). Forests of conifers dominated by the Araucariaceae and Podocarpaceae associated with pteridosperms, bennettitaleans, *Ginkgo* and/or cycads occurred over much of the continent, but cheirolepidacean conifers appear to have been more important in the vegetation of coastal regions and *Ginkgo* and cycadophytes in northern areas (Dettmann, 1994; Douglas, 1994). Cryptogam communities also varied across Australia, with more diverse ferns in the south-west, and greater development of lycopod communities about the river systems in the south-east and north-east (Dettmann, 1994).

Early angiosperms in Australia (latest Barremian–Cenomanian)

Angiosperms are first recorded in Australia during latest Barremian or earliest Aptian times (Fig. 61), with magnoliid taxa being the first present (Dettmann, 1994). The earliest occurring pollen (Barremian) are known from the Eromanga and Gippsland Basins and are referable to *Clavatipollenites*, which includes pollen comparable to that of *Ascarina* of the Chloranthaceae (Dettmann, 1986a; Burger, 1990). In the Gippsland Basin the pollen is associated with the oldest known flower branchlet which has been interpreted as representing a plant of prostrate herbaceous habit (Taylor & Hickey, 1990). Seeds tentatively assigned to the angiosperms (Douglas, 1963) are also an important part of this flora. Habitats of these early angiosperms included lakeside and riverine areas in the southern rift valley as well as the broad coastal plains adjacent to the estuary of the Eromanga Basin (Dettmann, 1994). Important macrofossils at this time include *Ginkgo australis*, which was widespread, and the spathulate-leaved pentoxylalean, *Taeniopteris daintreei*, which thrived in a range of habitats had leaves up to 200 mm in length (Douglas, 1994). Sometimes *T. daintreei* is accompanied by masses of seeds, and the pollen-bearing organ ascribed to this plant (*Sahnia laxiphora*) has been recognised from the well-known Koonwarra Fish Beds.

The earliest angiosperms represented in the Australian region probably migrated from a source in northern Gondwana or southern Laurasia (Muller, 1981; Dettmann, 1986a; Burger, 1990). Migration was more rapid than initially postulated (e.g. Dettmann, 1973) since there is only a brief time lag between latest Barremian/Aptian introduction in Australia and Hauterivian first appearances in the northern Gondwanan/southern Laurasian region (Brenner, 1984; Hughes & McDougall, 1986; Hughes, 1994). This evidence argues against Australia as a cradle region of the angiosperms (Takhtajan, 1969) and, further, provides little support for inception and diversification of earliest angiosperms on fragments of the Australian plate which rafted northwards during the Late Jurassic (Takhatjan, 1987). Radiation from the source region coincided with early opening of the North and South Atlantic Oceans, and it has been argued that associated environmental disturbances provided the trigger for dispersal (Dettmann, 1986b). The route to Australia may well have been via Antarctica and thence into southern Australia with the southern rift valley forming the

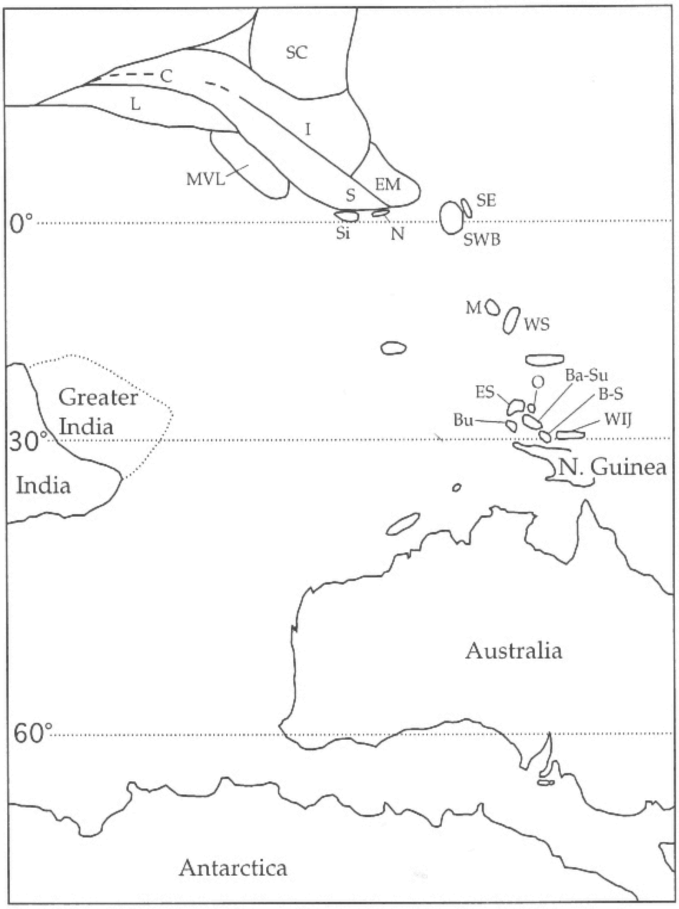

Figure 62. Speculative reconstruction of SE Asian terranes in relation to Australia for the Late Cretaceous (after Metcalfe, 1990). SC = South China; C = Changtang; L = Lhasa; I = Indochina; MVL = Mount Victoria Land; S = Sibumasu; Si = Sikuleh; EM = East Malaya; N = Natal; SE = Semitau; SWB = South West Borneo; M = Mangkalihat; WS = West Sulawesi; O = Obi-Bacan; ES = East Sulawesi; BU = Buton; Ba-Su = Bangai-Sula; B-S = Buru-Seram; WIJ = West Irian Jaya.

vehicle for floral channelling (Dettmann, 1986a, 1989). As noted earlier, migration from East Asia to northern Australia using a series of postulated microcontinents (Burger, 1981, 1990; Truswell *et al*., 1987) (Fig. 62) awaits substantiation, but theoretically provides a route for the ancestors of some important taxa (e.g. *Nothofagus* (Hill 1992; Hill & Dettmann, 1996; Hill, 1996). Modification of the vegetation associated with angiosperm invasion in Australia seems to have been more important in understorey communities than in canopy associations, with sporadic increases in hepatic and fern diversity occurring in the understorey (Dettmann, 1994).

With a major rise in sea levels during the early Aptian, shallow seas flooded the intracratonic basins, and the Australian landmass was reduced to several large islands, the eastern ones of which retained connections with Antarctica, the Lord Howe Rise, and the Queensland Plateau (Dettmann, 1994). In the forest vegetation of the interior basins podocarps were important canopy components, and the understorey included pteridosperms/bennettitaleans together with osmundalean and dicksonialean tree ferns, and communities of diverse terrestrial ferns (Dettmann, 1994). Angiospermous pollen is thus far unrecorded from the palynofloras, and flooding of the formerly broad coastal and lakeside plains may signify denudation of habitats of the early angiosperm invaders within the Eromanga Basin during the Aptian (Dettmann, 1994).

Podocarp forests and cheirolepidacean woodlands also occurred on the western island (comprising south-western areas of Western Australia), but knowledge of the vegetation is poor, except for the Perth Basin (Backhouse, 1988). Angiospermous pollen again has not been reported.

By contrast, coeval sediments in the Gippsland and Otway Basins contain *Clavatipollenites*, which confirms the presence of shrubby or herbaceous angiosperms in the south-east during the Aptian. The forests of the rift valley were floristically simpler than those surrounding the Eromanga, Surat and Perth Basins, where terrestrial ferns were more diverse and the Gleicheniales were abundantly represented (Dettmann, 1994). Moreover, the coastal vegetation of the Perth Basin included communities of Cheirolepidaceae, which were poorly developed about the inland seas and in the southern rift valley.

Near the Aptian/Albian boundary the inland sea retreated from the Surat and Maryborough Basins, and in the Eromanga Basin the eastern exit was closed and the southern limit advanced southwards. The south-western seaway extended east of the Officer/Eucla embayment to the Otway Basin where brackish conditions occurred in low lying areas. Volcanics were extruded in the Otway Basin, and non-marine deposition occurred in the Bass and Gippsland Basins (Dettmann, 1994).

A major vegetational change and the disappearance of several plant groups are recorded in the macrofossil record in the Otway Basin. Fossil assemblages are dominated by the osmundaceous fern *Phyllopteroides dentata* (often fossilised in company with its spore bearing organ *Cacumen*) and a new suite of araucarian and podocarp conifers (Douglas, 1994). Cantrill (1989, 1991) described several Araucariaceae taxa (seven foliage, one wood, and nine fertile organ taxa), three Podocarpaceae (one foliage and two wood taxa), and three Taxodiaceae (one foliage, one root and one wood taxon). *Geinitzia tetragona* (Taxodiaceae), associated with mycorrhizal rootlets in a palaeosol, is considered to indicate nutrient deficiency (Cantrill & Douglas, 1988). This vegetation prevailed over a much more subdued relief with flood plains prominent. *Ginkgo australis* was replaced by less digitate, smaller-leaved forms which may represent a distinct species. Terrestrial and aquatic ferns and hepatics prevailed in damp environments, and two small ferns with very long, narrow pinnae, *Alamatus bifarius* and *Amanda floribunda*, formed part of the community around the mud banks (Douglas, 1994). *Alamatus* bore oval sori in rows on each side of a main vein, while *Amanda* had unusual fertile spikes with sori in elongate clusters on modified pinnae. The angiosperms, although still rare at most outcrop localities, are represented by crenate leaved species, including the probably aquatic *Hydrocotylophyllum lusitanicum*, the first lanceolate leaf (Medwell, 1954) and cuticular debris in bore cores (Douglas, 1994).

Palynological evidence also indicates increasing regionalism of the Australian vegetation, and more widely distributed angiosperms (Dettmann, 1994). Angiosperms persisted in the south-east and, after retreat of the inland sea, were re-established in the Eromanga Basin and spread to the Surat Basin (Burger, 1990). Only chloranthaceous types are known, but the diversity had increased slightly within this group. The angiosperms probably colonised newly exposed areas, which were also invaded by aquatic, riparian and dry-zone communities of sphagnalean mosses and marsilealean, gleichenialean and schizaealean ferns (Dettmann, 1994). In the south-east portion of the Australian-Antarctic rift valley podocarp/araucarian forests persisted, but the floodplain flora expanded in response to widening of the river/lake systems. Even so, terrestrial and aquatic ferns were considerably less diverse than those of northern regions, and the vegetation retained a substantial lycopod component (Dettmann, 1994).

During the middle Albian the sea in the Eromanga/Surat Basins contracted further and was fringed by brackish lagoons and estuaries. Inundation of the Eromanga Basin by the sea occurred in the early late Albian, but the sea retreated again in the latest Albian with re-establishment of broad lagoonal and estuarine areas (Dettmann, 1994). To the east, coal-forming swamps occurred in depressions of the Maryborough and Styx Basins. The Eucla embayment was of lesser extent, but the easterly-extending estuary was flanked by rivers and lakes. River and lake systems also occurred in the Bass and Gippsland Basins (Dettmann, 1994).

Walkom (1919) described angiosperm leaves (*?Celastrophyllum* and *Phyllites* sp.) from the Styx Coal Measures in Queensland, but *Taeniopteris*, an indicator of Aptian or earlier deposits in the south-east, survives in this assemblage (and in the Cenomanian Winton flora, see below), which has caused some confusion about the age of these sediments. The Burrum Coal Measures assemblage of the Maryborough Basin in Queensland, which is the same age as the Styx assemblage (Day *et al.*, 1983), contains equisetaleans, *Ginkgo australis*, cycads and Araucariaceae similar to those of the Otway Basin (Douglas, 1994).

Palynological evidence confirms that non-magnoliid angiosperms were present in the Australian vegetation by the middle Albian and diversified rapidly during the late Albian (Burger, 1990; Dettmann *et al.*, 1992), and Burger (1993) recognised about 40 angiosperm species from pollen retrieved from the early to middle Cretaceous of the Eromanga Basin. Diversification was coincident with regression of the sea in the Eromanga/Surat Basins, and with widening of the floodplain in the southern rift valley (Dettmann, 1994). Precise affinities of the majority of non-magnoliid angiosperms are unknown, but *Tricolpites minutus* has an *in situ* association with fossil flowers of the Platanaceae in North America (Friis *et al.*, 1988). Several of the angiosperm pollen taxa have restricted distribution, and assemblages from northern areas of Australia are more diverse than those from the south-east (Dettmann, 1973; Burger, 1990). There are few data from Western Australia, but tricolpate angiosperm pollen occur in Albian sediments (Balme, 1964).

Cryptogams and gymnosperms also express regionalism at this time, particularly with respect to understorey communities (Dettmann, 1981; Dettmann & Thomson, 1987; Dettmann *et al.*, 1992). Community associations were also regionalised. Palynofloras of the intracratonic basins imply heathland and aquatic associations of diverse ferns, mosses and hepatics, whereas in the Styx and Burrum coal swamps the moss/hepatic element was poorly represented (Barnbaum, 1976). Understorey of the Otway Basin forests included dry-zone and aquatic ferns, hepatics and lycopods, but the ferns were less diverse and the gleicheniaceous types less prolific than in northern regions (Dettmann, 1994).

Early in the Cenomanian there was a major change in drainage systems and environmental patterns as Australia began to assume its present shape. Lakes and swamps developed in the Eromanga Basin after retreat of the sea. This was coincident with a major change in the tectonic regime when uplift was initiated along the eastern margin and subsidence occurred along the western margin. Seafloor spreading commenced along the southern margin, where marine conditions were established as far east as the Otway Basin. A lake system persisted in the Bass Basin, and to the east of the Gippsland Basin, the proto-Tasman Sea was initiated (Veevers *et al.*, 1991; Dettmann, 1994).

Palynofloras indicate that profound vegetational changes were associated with the dramatic changes in environment. In the south-east, riparian and aquatic communities appear to have been largely replaced by dry-zone associations. Notable is the increased diversity and representation of *Anemia* and *Selaginella*-type spores. Araucarian pollen is common and canopy associates of the araucarians included podocarps of the *Microcachrys*- and *Podocarpus*-type. *Classopollis* is occasionally frequent, implying the presence of cheirolepidacean woodlands. Magnoliid and non-magnoliid dicotyledonous angiosperms are represented by sulcate, tricolpate, tricolporoidate, and tricolporate pollen. Sulcate types similar to liliaceous monocotyledonous pollen are also present and there are rare grains of *Australopollis obscurus*, a form reminiscent of pollen of *Callitriche* (Macphail & Partridge, 1991).

There are notable differences between latest Albian–Cenomanian palynofloras from the south-east and those from the Eromanga Basin. The gymnospermous component of the Eromanga palynofloras includes a high proportion of podocarp pollen, and the cryptogam spore assemblages are more diverse and contain greater proportions of *Gleichenia*- and *Anemia*-type spores than those from the south-east (Dettmann, 1994). Abundant marsilealean, hepatic, and equisetalean and/or isoetalean spores are also present. Angiosperm pollen assemblages are similar to those of coeval sediments from the south-east but are more diverse with respect to the tricolpates, tricolporoidates and tricolporates, and contain *?Afropollis*, which includes pollen of winteraceous affinity (Doyle *et al*., 1990). However, *Callitriche*-type pollen has not been reported from the latest Albian–Cenomanian of the Eromanga Basin. Palynofloras similar to those of the Eromanga Basin are known from Bathurst and Melville Islands, north of Darwin, but they contain higher frequencies of *Classopollis*, *Balmeiopsis* and *Hoegisporis* (Burger, 1976). Brachyphyll pollen and common gleicheniaceous spores have been reported from the latest Albian–Cenomanian of the Perth and Eucla Basins (Balme, 1964; Ingram, 1968).

The palynological record confirms regional differences in the Australian vegetation during latest Albian–Cenomanian times (Dettmann, 1994). The Eromanga lakes and swamps were surrounded by conifer/cycad woodlands and heathlands of ferns. Lakes and swamps supported aquatic and littoral communities of ferns, fern allies, and hepatics. Angiosperms were probably distributed throughout these habitats. The Cheirolepidaceae appears to have been more strongly represented in coastal vegetation than in inland areas. Compared to the Eromanga Basin, the Otway and Gippsland Basins had less diverse fern communities and only slight development of aquatic communities. Cheirolepidacean conifers probably occurred in coastal sites, but the brachyphylls that shed *Hoegisporis* were poorly represented in the south-east.

A particularly important Cenomanian macrofossil flora occurs in the Winton Formation of central Queensland. Bose (1955) described equisetalean nodal diaphragms (*Equisetites* sp.), araucarian foliage-bearing shoots (*Araucaria* spp.), bark impressions, and detached taxodiaceous foliage-bearing twigs and cones (*Athrotaxis* sp.). In the next significant study of the flora, Peters & Christophel (1978) described permineralised taxodiaceous cones (*Austrosequoia wintonensis*) from a locality that also yields remains of various ferns, conifers and angiosperms. McLoughlin *et al*. (1995) described a diverse impression flora containing ferns (?Osmundaceae, Gleicheniaceae, *Cladophlebis*, *Sphenopteris*), *Ginkgo*, diverse conifers (including *Araucaria*, ?Podocarpaceae (*?Elatocladus*), Taxodiaceae (cf. *Austrosequoia wintonensis*) and one unknown form), *Taeniopteris*, and abundant leaves of eight species of angiosperms, all assignable to the Hamamelidae and possibly all with betulaceous and fagaceous affinities. This flora provides the first direct macrofossil evidence of the transition from gymnosperm- to angiosperm-dominated floras in Australia during the Cretaceous.

The forests and heathlands of the Aptian-Cenomanian grew at high latitudes, and the palynological evidence suggests that the forests mostly had a well-developed understorey and that the canopy would have had an open structure. Aptian palaeotemperatures of 12°C for the Eromanga sea (Stevens & Clayton, 1971) and 0–5°C for the Otway Basin (Gregory *et al*., 1989) confirm cool to cold climates, possibly with strong seasonality (Dettmann *et al*., 1992). Middle to late Albian palaeotemperatures signify warmer seas than for the Aptian. The highest value (16°C) is from the south-western Eromanga Basin where circulation was restricted. In the northern part of the basin, recorded temperatures (12°C) are similar to those reported from the Carnarvon Basin, Western Australia (Dettmann *et al*., 1992), although palaeotemperatures of Albian seawater from the Carnarvon Basin are approximately 7–11°C (Pirrie *et al.*, 1995). Cool to warm temperate climates with moderate to high precipitation occurred in the forested areas of the south-east and north-east, whereas in the Eromanga/Surat Basins, where there was extensive development of heathlands, rainfall may have been lower or seasonal (Douglas, 1986; Dettmann *et al.*, 1992).

Differentiation of Gondwanan elements and evolution of Australian elements (Turonian–Maastrichtian)

By the Turonian most of the continent was emergent. A river system developed in the former Eromanga Basin and drained south into the embryonic Southern Ocean, transporting sediment derived from the eastern highlands. Australia and Antarctica were linked through Tasmania, which separated the developing Southern Ocean on the west from the advancing Tasman Sea to the east. Lacustrine deposition continued in the Bass Basin and basalts were extruded in the Gippsland Basin (Veevers *et al.*, 1991; Dettmann, 1994).

Profound vegetational changes in both understorey and overstorey communities occurred in the south-east at about the Cenomanian/Turonian boundary. Some important components of extant austral floras appeared, such as *Lagarostrobos* and *Dacrydium* (Podocarpaceae). Early Proteaceae first occurred in the Turonian, followed by *Dacrycarpus* (Podocarpaceae) in the Santonian (Dettmann, 1994, Fig. 61). *Ilex*, which is now cosmopolitan, may have originated in the region (Martin, 1977). The podocarp/araucarian forest canopies probably included angiosperms, such as *Macadamia* and *Gevuina*/*Hicksbeachia* (Proteaceae; Dettmann & Jarzen, 1990)) by at least Santonian times (Dettmann, 1994). Angiosperm pollen assemblages increase steadily in diversity and there was considerable turnover of taxa among the cryptogams. *Ascarina*-type and liliaceous-like sulcate pollen occur infrequently, but *Callitriche*-type pollen is well-represented; aquatic and terrestrial herbs and shrubs were probably also present (Dettmann, 1994). Spores of hepatics and *Lycopodium* declined abruptly in diversity, whereas those of *Selaginella* increased. The fern component included *Lophosoria*, Gleicheniaceae, Osmundaceae and Marsileaceae, but Pteridaceae and Schizaeaceae were poorly represented. Several of these taxa migrated into the region during Turonian–Santonian times after earlier appearances elsewhere in Australia or southern Gondwana (Dettmann, 1994).

There are few published data from other areas. Sediments on Melville Island, off the Northern Territory coast, contain more diverse angiosperm pollen assemblages, but with several taxa in common with those from the south-east (Dettmann, 1973). Proteaceous-like pollen and abundant gleicheniaceous spores occur in Santonian spore-pollen assemblages from the Eucla Basin (Ingram, 1968).

During the Campanian and Maastrichtian, seafloor spreading continued along the southern margin, but Australia remained linked to Antarctica. Lakes occurred in the Bass Basin, and drained into the estuaries of the Gippsland and Otway Basins. The river system emptying into the Southern Ocean persisted, and a northward flowing river is believed to have developed in the Officer and Canning Basins. Igneous activity occurred along the eastern margin and may have been associated with the onset of seafloor spreading in the south-east and of rifting in the north-east. Emergent areas existed in the north-east linking Australia to eastern Papua New Guinea and New Caledonia (Dettmann, 1994).

Knowledge of the Australian Campanian-Maastrichtian vegetation comes mainly from the Gippsland, Otway and Bass Basins. Palynological data confirm that the area was forested, with components of the older (Turonian–Santonian) vegetation and newly introduced taxa. There were araucarians, diverse podocarps, *Nothofagus* (Nothofagaceae) for the first time, and increasingly diverse Proteaceae (Dettmann 1994).

Among the Proteaceae, several taxa (*Knightia*, *Macadamia*, *Bleasdalea*(=*Turrillia*), *Grevillea*) were probably in the canopy; others (*Carnarvonia*, *Telopea*, *Persoonia*) in the forest understorey; and yet others (*Stirlingia*, *Adenanthos*, *Beauprea*, *Beaupreopsis*) in sclerophyllous communities on forest fringes and/or nutrient deficient soils (Dettmann & Jarzen, 1991, 1996). Other rainforest associates included Winteraceae, *Ascarina*, *Ilex*

(Aquifoliaceae) and *Gunnera* (Gunneraceae). Pollen that may represent *Clematis* (Ranunculaceae), Trimeniaceae, *Callitriche* (Callitrichaceae), and Epacridaceae also occur (Dettmann & Jarzen, 1990; Dettmann, 1994). The cryptogam flora included mosses, hepatics and diverse selaginellids. Gleicheniaceae, Osmundaceae, *Culcita* (Culcitaceae), *Blechnum*/*Doodia* (Blechnaceae), *Pteris* (Pteridaceae), *Actinostachys* (Schizaeaceae), and possibly *Azolla* (Azollaceae) were represented in fern communities (Dettmann, 1994).

A site near the Olgas in central Australia has palynofloras rich in Proteaceae associated with less frequent podocarps and very rare *Nothofagus* (Twidale & Harris, 1977; Harris & Twidale, 1991). *Gunnera* pollen and microsporangia of ?*Azolla* are also present. Another site, in the Capricorn Basin off the central Queensland coast, contains common Casuarinaceae pollen and fern spores associated with rare *Clematis*-type pollen in assemblages that are questionably of latest Cretaceous age (Hekel, 1972). The vegetation of these northern sites was distinct from that in the south-east, but it is uncertain whether these dissimilarities represent geographic or age differences.

During the Turonian–Maastrichtian, Australia slowly drifted northwards and by the close of the Cretaceous the south-east was at latitudes of 65°S. Evidence for climates of the Turonian is conflicting; a single ammonite from the Otway Basin provided a palaeotemperature of 28°C (Dorman, 1966), but associated foraminiferal faunas indicate cold waters (Taylor, 1964). Palynological evidence confirms forests dominated by Podocarpaceae, which probably had an open canopy structure. During the Santonian-Maastrichtian, proteaceous trees (*Knightia*, *Macadamia*, *Bleasdalea*) were represented in the canopy. The cool temperate conditions implied by palaeotemperature determinations (16.5–19°C) and foraminiferal faunas (Dorman, 1966; Taylor, 1964) indicate tall open-forests (up to 30 m in height) with canopy taxa (mainly podocarps and Proteaceae, but also rare *Nothofagus* subg. *Brassospora* having conical-shaped crowns and coriaceous, notophyll-sized leaves (Specht *et al*., 1992). An open-forest structure at the high latitudes would allow some light to penetrate to a shrubby understorey of Proteaceae (*Carnarvonia*, *Telopea*), Winteraceae, Trimeniaceae and *Ilex*, and a ground stratum of diverse cryptogams. Many of the taxa represented in the Late Cretaceous open-forests survive today in closed-forests (rainforests) in the Australasian flora and some (e.g. *Dacrydium*, *Dacrycarpus* (Podocarpaceae), and *Knightia*, *Bleasdalea*, *Macadamia* and *Carnarvonia* (Proteaceae)) are restricted to north-eastern Australasia (Dettmann, 1994). She noted that although rarely dominant in present-day perhumid forests, canopy taxa with a Cretaceous history have slender, conical crowns that are sometimes emergent above the dominants which have spreading, dome-shaped crowns. Dettman speculated that, as Australia drifted into lower latitudes during the Tertiary, the gaps between the canopy taxa of the Cretaceous forests were filled by invasive or newly evolved autochthonous taxa with growth habits that maximised solar absorption in mid to low latitudes.

Cretaceous–Tertiary (K–T) boundary event

There are no well exposed Cretaceous–Tertiary boundary sections in Australia, and hence no evidence in the form of the iridium layer or otherwise of a catastrophic event at this time. There is also scant palaeobotanical evidence for the effect of the K–T boundary event in Australia. Wolfe (1991) concluded that the impact event which caused mass extinction at the K–T boundary occurred in June, based on the reproductive stage reached by fossil aquatic plants in the Northern Hemisphere. He noted that the 'impact winter' had little effect on the land biota at high southern latitudes, which were, by his argument, in mid-winter. Many deciduous plants were present at high southern latitudes at this time, and they would have been in a leafless, dormant state, while evergreen plants at these high latitudes would have been in a dormant phase. Wolfe (1987) predicted that if mesothermal vegetation had been devastated in the Southern Hemisphere by an 'impact winter', a rise to dominance of *Nothofagus* might be expected. However, he noted that in inferred mesothermal regions, Paleocene palynofloras represent a diverse forest containing taxa that are now exclusively evergreen. This, along with evidence on the vulnerability of modern wood tissues to freezing, led Wolfe to conclude that no effect of an 'impact winter' can be detected in Southern Hemisphere vegetation. Wolfe's scenario explains the lack of evidence to date for the effect of the K–T impact on high southern latitude vegetation. However, some of the assumptions made by Wolfe (1987) in reaching his conclusion have now been questioned. It is important to recognise that there are fundamental differences between the floras of the Northern and Southern Hemispheres and these differences have a complex history, which cannot be attributed to a single cause, no matter how catastrophic it may have been (Hill & Scriven, 1995).

Bore core macerations and microfloras indicate that many of the angiosperm families that achieved prominence as the Tertiary proceeded were present in the latest Cretaceous. Although available evidence indicates that the vegetation was modified considerably at or near the Cretaceous/Tertiary boundary (Helby *et al.*, 1987), Dettmann (1994) concluded that a mass extinction event is not evident. She noted that many of the Cretaceous taxa range into the Tertiary, but some have broken stratigraphic ranges involving the Paleocene. This phenomenon has been interpreted as indicating short distance retreat of the plants during the earliest Tertiary, followed by advance during latest Paleocene-Eocene times (Dettmann & Jarzen, 1991). Causative mechanisms may have involved alterations to drainage patterns near the close of the Cretaceous. However, Macphail *et al.*, (1994) noted an apparently massive impoverishment of the angiosperm flora at the K–T boundary and a possibly related major expansion of gymnosperms, which they believed was best interpreted in terms of mass extinction.

Macrofossil data are almost non-existent. Although there has been no systematic examination of cores from the 40 or so bores that may provide information on Cretaceous–Tertiary boundary events in the Otway Basin, preliminary observations reveal no macrofossil changes anywhere near as marked as those between zonations within the Cretaceous recognised by Douglas (1969).

Southern mid–high latitudinal phytogeographic region; source and dispersal corridor of austral plants

Close floral relationships existed between Australia and associated high latitudinal areas of southern Gondwana throughout the Cretaceous (Dettmann, 1981, 1986b; Dettmann & Thomson, 1987; Dettmann *et al.*, 1992) in the Southern Gondwana Floristic Province (Brenner, 1976) (also known as the Weddellian Biogeographic Province (Case, 1989)). This region was characterised by a series of podocarp/araucarian forests, and was invaded by early angiosperms during latest Barremian–Aptian times from a source in northern Gondwana. In the Antarctic Peninsula/South American region, floral zonation across the latitudes was steep with an interfingering of austral podocarp/araucarian and northern Gondwanan cheirolepidacean communities (Dettmann, 1986b, 1994), the geographical limits of which fluctuated during opening and enlargement of the South Atlantic, Indian, and Southern Oceans (Dettmann & Thomson, 1987).

The Cretaceous pre-angiospermous vegetation of southern Gondwana was characterised by regionalism within both overstorey and understorey associations, which is believed to have been influenced by climatic as well as topographic and edaphic factors (Dettmann, 1986b, 1994; Askin, 1989). Associated with the canopy of podocarps and araucarians were ginkgos, cycads, taeniopterids, pteridosperms and bennettitaleans together with ground communities of ferns, lycopods and bryophytes. In northern areas (India, Patagonia, northern Australia), araucarians were more important in the canopy than the podocarps, and cycads were more plentiful in interior and northern coastal areas than ginkgos which appear to have preferred more humid habitats (Dettmann, 1994). Cryptogam associations also varied across southern Gondwana; fern spores are more plentiful and diverse in what were coastal regions, whereas lycopods (mainly *Lycopodium*) thrived in inland areas. Spores of sphagnalean mosses and hepatics have greater abundance in depositional basins in low-relief compared with high-relief terrains (Dettmann, 1986b, 1994).

As the oceans opened, disturbances to adjacent land areas appear to have been the driving force for floral evolution and exchange (Dettmann, 1989; see earlier discussion). Many taxa migrated to Australia after originating elsewhere, and migration was predominantly in an easterly direction in the southern Gondwanan assembly, with South America, India, and

Antarctica being crucial migrational pathways during the earliest Cretaceous (Dettmann, 1994).

Evidence for angiosperm introduction into Australia suggests routes involving southern Gondwana, and radiation was contemporaneous with opening of the South Atlantic and Indian Oceans. As was typical of southern Gondwana, the first angiosperms to arrive in Australia were herbaceous or shrubby chloranthaceous taxa, which would have competed with taxa in the shrubby strata at forest fringes, or those of the understorey within the forests (Dettmann, 1994). The latest Barremian–Aptian vegetation existed under cool to cold, humid climates, and the forests had open canopies (Creber & Chaloner, 1987; Specht *et al.*, 1992).

A second wave of angiosperms migrated to Australia during middle Albian–Cenomanian times and involved non-magnoliid dicotyledonous taxa whose lineages evolved in northern Gondwana near the Barremian/Aptian boundary (Brenner, 1976; Doyle *et al.*, 1982). Once again, migration was in an easterly direction, involving southern South America and Antarctica. India became isolated from the southern Gondwanan assembly, and the meagre information on its mid-Cretaceous vegetation suggests that its floral links with Australia had diminished (Dettmann, 1992). Temperatures were warmer at this time in Australia than for the Aptian, but precipitation may have been less or seasonal in interior regions. By the Cenomanian Australia had commenced its slow drift north (Veevers & Eittreim, 1988), but remained in high southern latitudes where the forests would have had an open structure. Niches occupied by the non-magnoliid dicotyledons included shoreline and floodplain situations, but distribution patterns of the two separate pollen associations delineated by Burger (1990) imply that some of the angiosperms were established in the open forests of hinterland regions of the Eromanga Basin. Near the Cenomanian–Turonian boundary angiosperms with pollen similar to *Callitriche* were introduced into the vegetation of the southern rift valley. *Callitriche*, which today occupies aquatic and semi-aquatic habitats, may well have had its origins in northern Gondwana (Herngreen, 1973; Dettmann, 1994).

During the Albian–Cenomanian Australasia, Antarctica, southern South America and the Falkland Plateau retained connections and formed the southern Gondwana assembly at high southern latitudes. As the South Atlantic Ocean opened, forests advanced over the Falkland Plateau and partially replaced the cheirolepidacean communities. Here, and on the Antarctic Peninsula, the forests were associated with ginkgos/cycadophytes, pteridosperms and diverse terrestrial ferns, several of which are unknown from Australasia (Dettmann & Thomson, 1987). Other taxa had restricted geographic ranges within the southern Gondwana region. Thus, for example, the brachyphyll that shed *Hoegisporis* was restricted to northern and western areas of Australia where the flora was richer in angiosperm, fern, and hepatic taxa than the vegetation of south-eastern Australia (Dettmann, 1994). Cheirolepidacean conifers were well represented in northern coastal areas, but were only locally developed about the estuary in the south-east rift valley.

During the remainder of the Cretaceous (Turonian–Maastrichtian), angiosperms continued to migrate into Australia from northern Gondwana, but many newly introduced taxa differentiated from northern Gondwanan lineages in the Australasian-Antarctic region. Northern Gondwanan origins have been demonstrated for *Gunnera* (Jarzen & Dettmann, 1989) (Fig. 63), and *Belliolium*/*Bubbia* (Winteraceae) may have evolved in the same region (Dettmann & Jarzen, 1990). Pollen that may represent earliest Proteaceae occur in the Cenomanian-Turonian of northern Gondwana (Muller, 1981), but subsequent Late Cretaceous diversification of the Proteaceae was centred in southern high latitudes (Dettmann & Jarzen, 1991). Four of the seven subfamilies of extant Proteaceae are represented in the Campanian-Maastrichtian pollen record of the Austro-Antarctic rift valley (Dettmann, 1994). Diverse assemblages of proteaceous pollen recorded from the Otway Basin, south-eastern Australia includes taxa aligned to *Adenanthos*, *Beauprea* and *Beaupreopsis* (Proteoideae), *Persoonia* (Persoonioideae), *Carnarvonia* (Carnarvonioideae), and *Grevillea*, *Telopea*, *Macadamia*, *Bleasdalea* and *Knightia* (Grevilleoideae) (Dettmann, 1994; Dettmann & Jarzen, 1996). Diversification of the family coincided with habitat changes associated with early opening of the Southern Ocean (Fig. 64). This region may also have been the centre of origin of *Ilex* in the Turonian (Martin, 1977) and of lineages of the Trimeniaceae and Epacridaceae in the Campanian (Dettmann & Jarzen, 1990).

Lagarostrobos, Dacrydium and *Dacrycarpus* (Podocarpaceae) and *Nothofagus* (Nothofagaceae), which are important elements of austral temperate rainforests, first appeared in the Austro-Antarctic region during the Late Cretaceous (Dettmann *et al*., 1990, 1992). The podocarps had successive introductions during Turonian–Santonian times, and ancestral *Nothofagus* appeared in the Campanian. Over the years there has been considerable debate concerning the centre of origin of *Nothofagus* or its immediate ancestor in particular, and this was recently summarised by Hill (1992, 1994a) and Hill & Dettmann (1996). The most probable options now seem to be southern South America/Antarctic Peninsula, or SE Asia. Although there is considerable doubt about these centres of origin, the fossil record is very clear on the evolution and diversification of *Nothofagus* (Fig. 65). Differentiation of *Nothofagus*, and appearance in the fossil record of its four extant subgenera occurred during the late Campanian-Maastrichtian in the southern South America/Antarctic Peninsula region. Diversification was concurrent with volcanic and tectonic activity under climates that were cooler than those of southern Australasia, the Late Cretaceous diversification centre of the Proteaceae. Extant lineages of *Nothofagus* migrated to Australia during the latest Cretaceous–Palaeogene and routes must have involved Antarctica (Dettmann *et al*., 1990). The same route may have been followed by the Myrtaceae, Olacaceae, Loranthaceae and Sapindaceae (Dettmann, 1994). Antarctica probably served as a dispersal route for several other taxa, with migration in the opposite direction, including several Proteaceae and Epacridaceae that were in Australia prior to their latest Cretaceous–Tertiary arrival in western Antarctica (Dettmann, 1989; Askin, 1989).

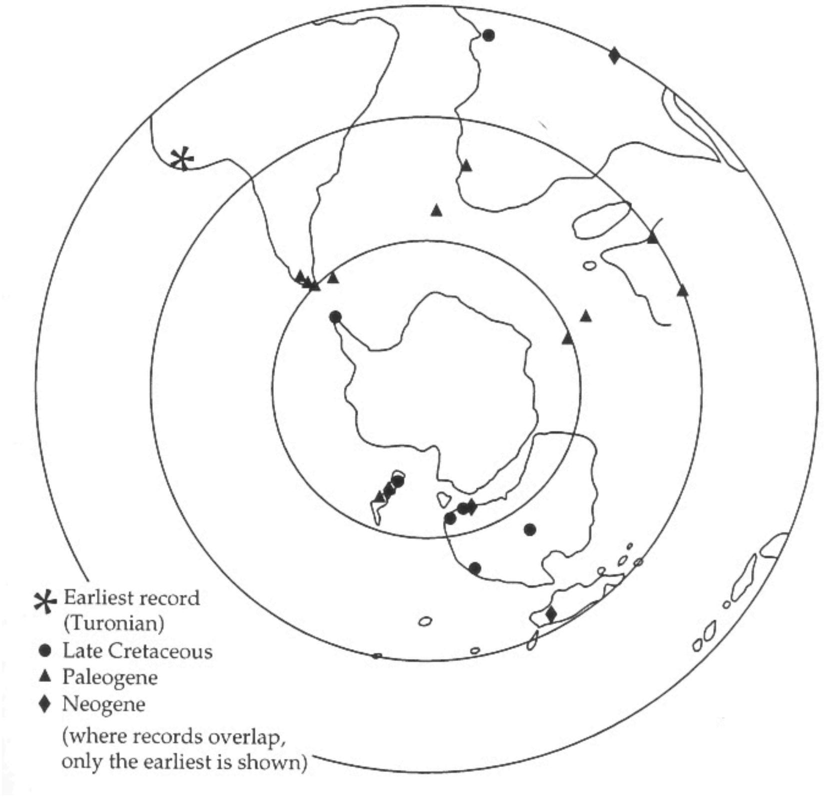
✱ Earliest record (Turonian)
● Late Cretaceous
▲ Paleogene
♦ Neogene
(where records overlap, only the earliest is shown)

Figure 63. Palaeogeographic reconstruction of the Southern Hemisphere at about Late Cretaceous time, showing the fossil distribution of *Gunnera*. Modified from Hill & Scriven (1995), with data from Jarzen & Dettmann (1989) and Dettmann & Jarzen (1990).

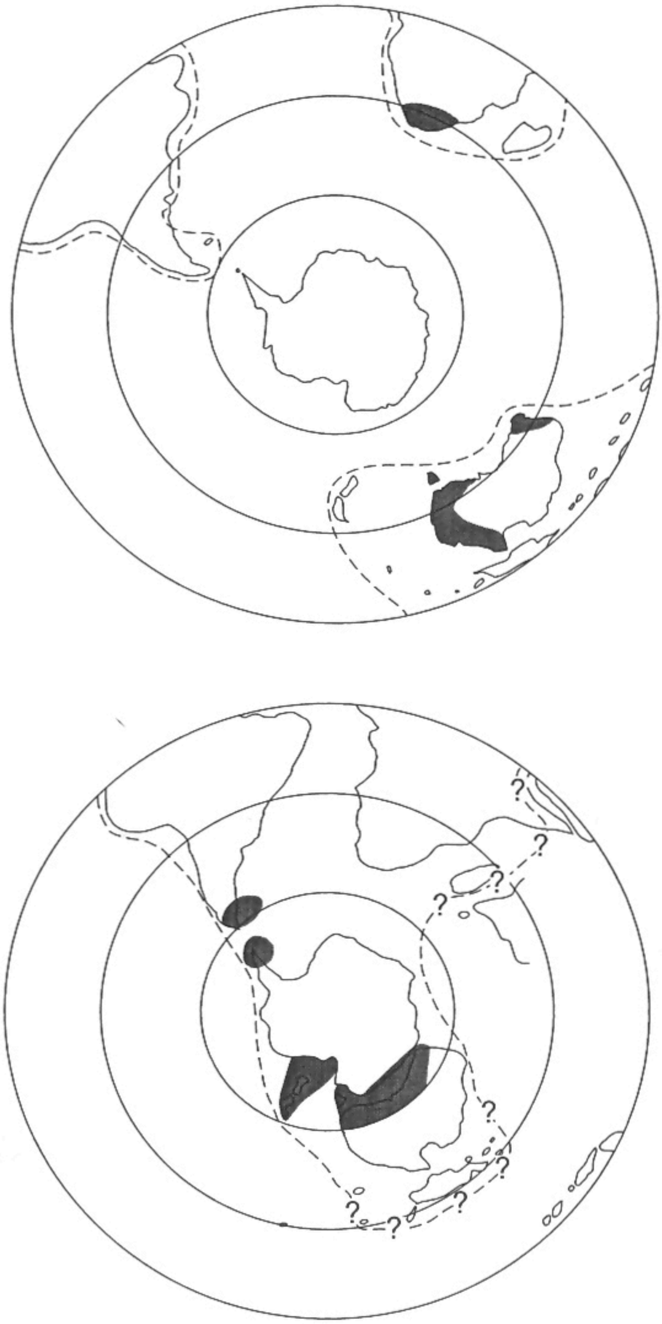

Figure 64. Present and Cretaceous distribution ranges of the Proteaceae plotted on south polar projections for the present (top) and Santonian (bottom). The known range is indicated by a broken line, and question marks indicate an inferred range. Shaded areas mark areas of greatest concentration. Modified from Dettmann & Jarzen (1991).

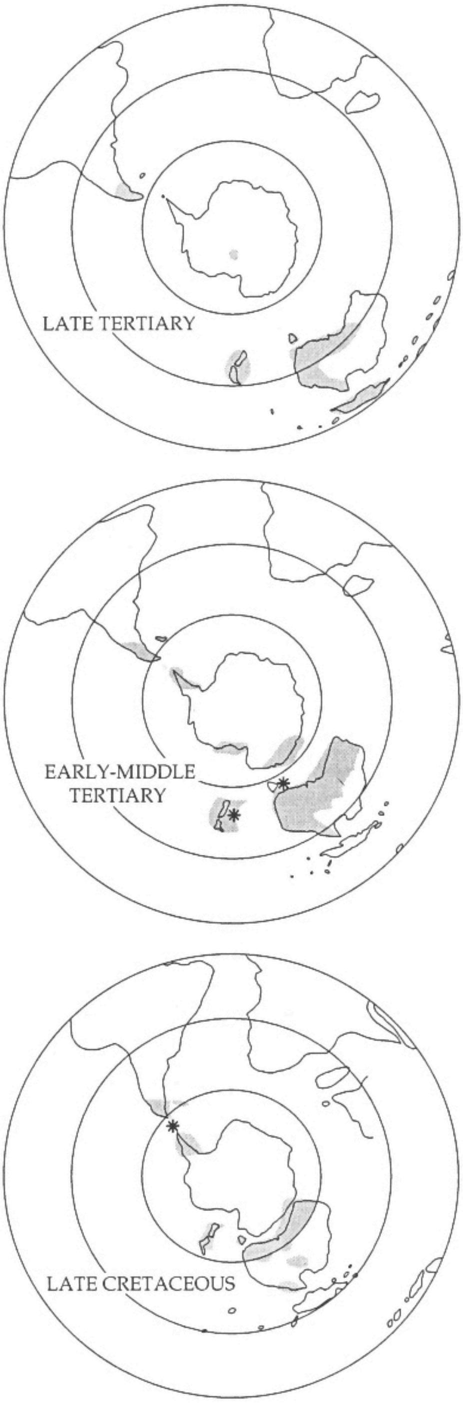

Figure 65. Distribution of *Nothofagidites* pollen plotted on south polar projections (* = diversification centre). After Hill & Dettmann (1996).

Truswell *et al*. (1987) postulated that several of these elements (Olacaceae, Sapindaceae, Myrtaceae) may have been introduced to northern Australia using 'stepping stones' from SE Asia (Fig. 62). Dettmann (1994) concluded that this route is not supported by the pollen record for the Olacaceae and Sapindaceae, but should not be dismissed for the Myrtaceae.

The pollen record demonstrates that several important elements of the modern vegetation were established by the close of the Cretaceous. Most were derived from Gondwanic stock; some evolved in northern Gondwana, and others in the Austro-Antarctic region (Dettmann, 1994). Many of these taxa are now associated in rainforests, but several (*Adenanthos*, *Stirlingia* and some Epacridaceae) are restricted to nutrient deficient soils in the Mediterranean climatic region of southern Australia, implying that sclerophylly in the Australian vegetation dates to the latest Cretaceous (Dettmann, 1994).

The southern Gondwanan Late Cretaceous vegetation was strongly regionalised within the same latitudinal belt and across the latitudes (Dettmann, 1994). The Proteaceae was important in central Australia, but at higher southern Australian latitudes (60–65°S) both Podocarpaceae and Proteaceae were well-represented in the canopy of open-forests (Specht *et al*., 1992). Forest understoreys included shrubby Proteaceae, Winteraceae, Trimeniaceae and *Ilex,* as well as a ground stratum of diverse ferns (Dettmann, 1994).

Summary of Cretaceous vegetation

It is clear that the southern Gondwana vegetation, including that of Australia, was floristically heterogeneous throughout the Cretaceous. Much of the area was forested, but woodlands, heathlands, and aquatic communities also occurred. The high latitude forests had an open structure, podocarps and araucarians were important canopy components, and these two families were established in Australia well before the Cretaceous. Herbaceous and shrubby angiosperms invaded understorey communities fringing and associated with the earliest Cretaceous forests during the latest Barremian–Aptian, and angiosperms had entered the canopy by the Santonian. This mid-Cretaceous interval saw the extinction or marked decline of a number of previously prominent gymnosperm and cryptogam groups, notably Bennettitales, Pentoxylales, *Pachypteris*, *Thinnfeldia*, *Rienitsia*, cheirolepidacean conifers, ginkgophytes and equisetaleans. It is not yet clear whether these extinctions were driven by changes in the physical environment or by competition from the newly arriving angiosperms, and this is an important problem for future research. Australia occupied a peripheral position in the southern Gondwana assembly, and routes traversed by the earliest angiosperm invaders from northern Gondwana predominantly involved other landmasses in the assembly with perhaps some input from SE Asia. The first migratory wave of magnoliid angiosperms occurred no later than the latest Barremian, and was coincident with lowered global sea levels, and early opening of the South Atlantic and Indian Oceans (Dettmann, 1994).

A subsequent angiosperm invasion during the middle Albian–Cenomanian included non-magnoliid lineages that evolved in northern Gondwana during the Aptian. Once again, angiosperms invaded shoreline communities after regression of the Aptian sea in intracratonic basins and widening of the flood plain of the Austro-Antarctic rift valley. Angiosperm migration from northern Gondwana continued during the Turonian–Maastrichtian and was concurrent with *in situ* evolution and differentiation of austral groups in the Australian-Antarctic region. Two loci of evolution and diversification have been identified. Areas surrounding the embryonic Southern Ocean were a diversification centre of the Proteaceae and may have been the place of genesis of *Ilex*. The region including southern South America and the Antarctic Peninsula was a diversification centre of early *Nothofagus* during phases of volcanic and tectonic activity.

The pollen evidence counters Takhtajan's (1969) argument that Australia was a centre of origin for early angiosperms, and supports the hypothesis of Webb *et al*. (1986) that Australian rainforests are remnants of a heterogeneous Gondwanan flora, although perhaps with some Asian input. Evidence for the evolution of sclerophylly is also found in the Late Cretaceous pollen record. The sclerophyllous taxa probably formed communities on low nutrient or waterlogged soils on forest fringes (Specht *et al*., 1992).

The Australian Cainozoic

There have recently been major advances in our understanding of the environments of the Cainozoic in Australia. These can be identified in a number of different categories of research and include, from the geological side, a better understanding of the Tertiary timeframe, more data and fresh syntheses of sedimentary environments, and an enhanced understanding of the tectonic setting of Australia within the region. The quantity and the quality of palaeoclimatic and palaeontological information has also increased dramatically recently. Some of these developments are discussed in detail in other chapters, but a brief comment on some is informative here.

The Tertiary timescale

Refinement of the timescale for the Australian Cainozoic has been an ongoing problem since the first marine fossils were identified last century (Truswell, 1993). Standard reference sections for the global Tertiary were established in the Northern Hemisphere, at first with the standard sequences and stages of the Tertiary in Europe, and later, with the development of global timescales for marine planktonic faunas in the Neotropics. There has been considerable effort to relate Australian sequences to these standards, and this has been greatly assisted by using local faunal events in marine sections (e.g. the first and last appearances of planktonic foraminiferal species) and correlating these, with some hesitation, with scales such as the P and N zones (global reference zones based on evolution of taxa within tropical planktonic foraminifera and nanoplankton lineages).

Australian palynological zones, based both on pollen and dinoflagellates, have been erected in southern Australian coastal basins where it has been possible to link them to the local marine sequences. These in turn have been correlated, often tenuously, with international zonal standards. This correlation has been further complicated because Tertiary biostratigraphers have not yet reached agreement on a standard calibration for the timescale in terms of millions of years.

It is still difficult to date sequences of terrestrial origin in Australia. The standard zones have been established in southern coastal basins, and there is still uncertainty concerning just how far away from these basins the zones can be recognised with confidence. This is an issue in trying to establish the age of sediments in the Murray Basin and in central Australia.

There has been some calibration of palynological zones against isotopically dated volcanic rocks in the Eastern Highlands of mainland Australia and Tasmania, where fossil-bearing deposits are interbedded with, or underlie, basalts. Unfortunately, for large parts of the continent there are no basalts. Palaeomagnetic techniques have also been used to calibrate the age of fossil floras. In Lake George, in southern New South Wales, Pliocene pollen-bearing sediments have been dated by magnetic reversal stratigraphy, and in central Australia Tertiary sequences have been related to a Cainozoic polar-wander curve derived from successive positions of the palaeo-pole through the interval (Truswell, 1993). However, despite these efforts, the dating of many fossil-bearing sequences remains a major obstacle to resolving some of the key issues in Australian vegetation history.

Regional geologic framework

The sequence of separation of Australia from the rest of Gondwana is now understood in considerable detail, with current knowledge on the timing of the separations of Australia and Antarctica and Australia and New Zealand summarised by Veevers *et al.* (1991).

The pattern of major tectonic events to the north of Australia is also better understood. It is now believed probable that slivers of continental crust have repeatedly rifted away from Australia's northern margin between the late Palaeozoic and Cainozoic and have become embedded within SE Asia. However, in most cases the precise timing of these rifting and collision events remains problematic. Nevertheless, a clear understanding of the geological history of this region is of immense importance in understanding the phytogeographic relationships between Australia and SE Asia. Information crucial to biology, such as where the areas of emergent land might have been at particular times in the past is difficult to find, but is likely to represent a major field of research in the near future.

Another facet of geological information which is significant for vegetation (and climatic) history concerns the elevation of Australia's eastern highlands. After decades of controversy, reliable geological information now suggests that this region showed considerable elevation by the beginning of the Tertiary (Truswell, 1993). In the south-eastern highlands, there may have been as much as 800 metres of relief by the Paleocene (Taylor *et al.*, 1990). Such information provides a framework for interpreting possible altitudinal stratification of vegetation during the Tertiary.

Palaeoclimatic data

In dealing with palaeoclimates, it is important that information drawn from outside the vegetation record is clearly separated from that drawn from the plant fossils themselves, in order to avoid a circularity of argument. Sea-surface temperature is one of the important parameters in climatic reconstruction. There is now available a detailed estimate for sea surface temperatures off north-eastern Australia (Fig. 66) that shows temperatures for the Tertiary in the vicinity of the Coral Sea and Queensland Plateau. It has been built by extrapolating oxygen isotopic data from sites in the western Pacific, using latitudinal temperature gradients estimated for 19 time intervals during the Cainozoic. These are thus deduced temperatures.

The curve shows the effects of global cooling during the Palaeogene, and it also records the effects of the northward passage of the Australian plate. The decreasing temperatures during the early Tertiary reflect a high-latitude cooling trend that was global in its impact. In this part of the curve, peak warming in the early Eocene is followed by cooling into the Oligocene. The remainder of the curve reflects the passage of north-eastern Australia first into subtropical water masses and then into the tropical zone. It is interesting to note that, for the central part of the Great Barrier Reef, coral reefs did not begin to develop until tropical water masses were encountered in the Pliocene.

The north-eastern Australian curve describes conditions in areas well offshore. Another curve, developed for Victorian coastal sequences (Fig. 67), shows more local expressions

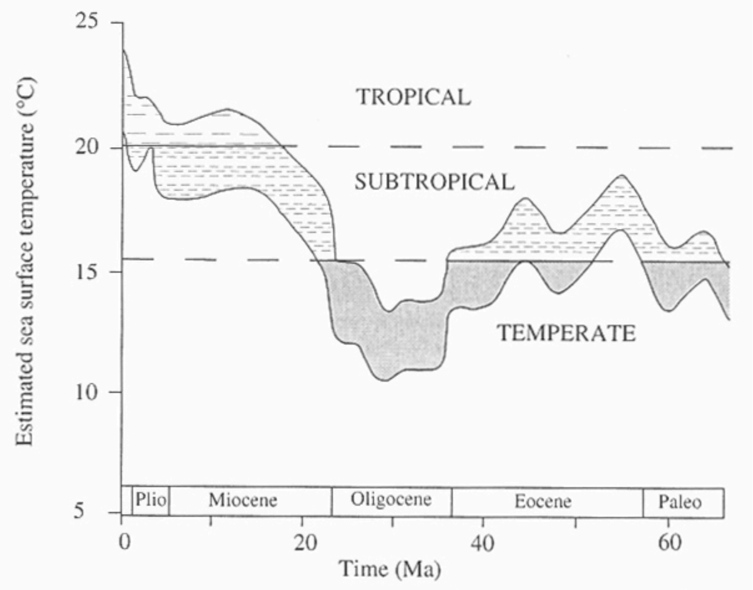

Figure 66. Sea-surface temperatures for north-eastern Australia during the Cenozoic. Simplified from Feary *et al.* (1991).

of global events. There are pronounced temperature drops across a short interval near the Eocene-Oligocene boundary; these are the culmination of declines in sea-surface temperatures that began earlier, probably about the middle Eocene. Locally, these temperature drops were followed by warming in the early Oligocene. Just how far afield these effects were felt is problematic, especially when recent evidence suggests that the first glaciations in Tasmania occurred in the early Oligocene (Macphail *et al*., 1993).

It is more difficult to obtain quantitative palaeoclimatic data from terrestrial areas than it is from the marine realm. There have, however, been some attempts recently to quantify past climatic conditions on the basis of palynological assemblages, using the BIOCLIM database (see Kershaw & Nix, 1988). This methodology has been applied to pollen suites from the Paleocene and Eocene of the Eyre Formation in south-central Australia (Sluiter, 1991). On the assumption that climatic profiles have remained constant for key taxa, Sluiter estimated that the mean annual temperatures for the region were of the order of 18–19°C, with annual precipitation in excess of 1400 mm in the late Paleocene, and slightly higher in the Eocene.

Mean annual temperatures are only one facet of climatic controls on plant growth; the effects of variability are of equal, perhaps greater, importance. Ecophysiological studies of living genera, notably *Nothofagus*, have made a significant contribution to our understanding of the way in which climatic influences have acted to redistribute taxa that were mutually associated in the early Tertiary. The fossil record provides an empirical history – a series of snapshots – of what grew where at different intervals: the ecophysiological work, such as that undertaken by Read and others (e.g. Read & Hill, 1985, 1988, 1989; Hill *et al*., 1988; Read & Hope, 1989; Read & Busby, 1990; Read *et al*., 1990) provides possible reasons for the observed changes.

Other approaches to estimation of palaeoclimate include analysis of foliar physiognomy (leaf size, shape and margin type) and type and distribution of epiphyllous fungi. The former approach has been used extensively in Australia (e.g. Christophel & Greenwood, 1987a, 1989), but there is substantial doubt over the error incorporated in the results (Jordan, 1997). Epiphyllous fungi appear to offer great potential as a reliable method for determining rainfall (both amount and annual distribution), but so far only preliminary research has been carried out (e.g. Lange, 1976, 1978a; Wells & Hill, 1993).

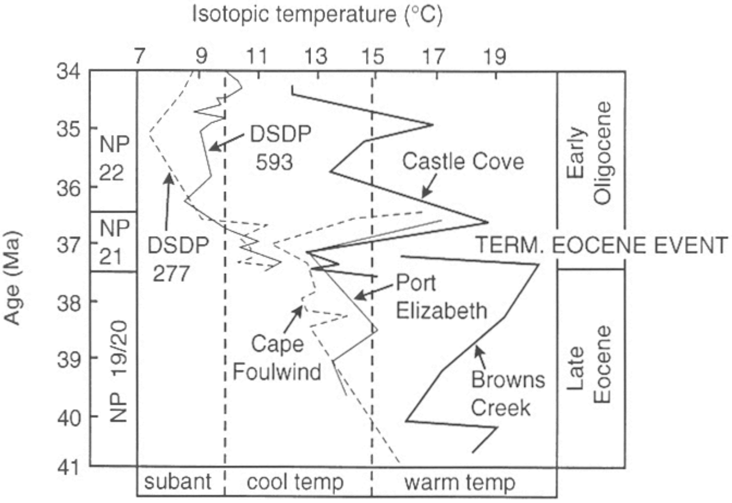

Figure 67. Late Eocene–early Oligocene sea-surface temperatures. The chronological scale on the left with NP zonal units is for nannofossils. The solid line on the right shows temperatures derived from coastal sequences at Browns Creek and Castle Cove in Victoria. Modified from Kamp *et al*. (1990) and Truswell (1993). (DSDP = Deep Sea Drilling Project, NP = Nannoplankton; Term. Eocene Event = Terminal Eocene Event, subant = subantarctic, cool temp = cool temperate, warm temp = warm temperate).

Major vegetation trends in the Tertiary

The main trends in the development of Australian vegetation types during the Tertiary can be identified by focussing on one or two key sites for different time intervals. These are only snapshots of vegetation events for particular intervals of time, and are of necessity selective, but provide at least an outline of important trends.

Palaeocene

At this time Australia was in the early phases of separation from Antarctica, and its southern margin lay at about 70°S, with new seafloor beginning to be generated in the older rift valley separating the two continents (Veevers *et al.*, 1991). Some union still lingered in the region of the South Tasman Rise. It was a phase of warming after the cooling of the Late Cretaceous, with temperatures higher than those of today. The relief of the continent was much as it is at present (BMR Palaeogeographic Group, 1990), but there were extensive river systems on the west Australian shield, carved probably during the Cretaceous, and there were thin sand sheets spread by braided rivers in the east (perhaps by sheet flooding) and continued volcanism in the eastern highlands.

There are palynological sites from northern Tasmania, through the Bass, Otway and Gippsland Basins up to the south-eastern highlands of New South Wales, extending possibly to the northern tablelands, through the Murray Basin and into the centre in the Lake Eyre Basin (Truswell, 1993). Paleocene spore-pollen assemblages have also been recovered from subsurface samples of the Kings Park Formation in the Perth area (Truswell, 1993). A single macrofossil site is known in the south-eastern tablelands (Taylor *et al.*, 1990).

An impression of the vegetation can be gained by reference to sites in the south-eastern highlands. A number of sites occur in this broad region, centred on Bombala, where lake sediments preserved between basalt flows have yielded pollen, a great deal of beautifully silicified wood and leaf floras. These were montane sites, with probably about 800 m of regional relief (Taylor *et al.*, 1990). In the pollen suite about 60 taxa have been identified. The suite is dominated by conifers, by Podocarpaceae in particular, including *Podocarpus*, *Dacrydium* and, very commonly, pollen of the *Lagarostrobos* type. The latter includes both the *L. franklinii* morphotype (now restricted to a monospecific genus on Tasmania's west coast) and a range of related species now extinct. Araucariaceae pollen is present in most samples, as *Araucariacites* and *Dilwynites*. It is interesting to note that *Dilwynites* pollen is being placed in the same lineage as the recently described Wollemi Pine (*Wollemia nobilis*, Jones *et al.*, 1995), due to an ornamentation consisting of scattered granules. The match, however, is not perfect since granules and tuberculae characterising the two described fossil species (*D. granulatus* and *D. tuberculatus*) are much more robustly developed than in *Wollemia nobilis* pollen (Macphail *et al.*, 1995; M.K.Macphail, *pers. comm.*). *Phyllocladus* and *Microstrobos* are also present. For the angiosperms, the ancestral form of *Nothofagus* (*Nothofagidites senectus*) is most common, but there are other *Nothofagus* species too. *Ilex* and Casuarinaceae are present and there are extinct taxa represented by pollen types with no modern affiliates.

At the generic level, the thermal responses of descendant taxa suggest vegetation in the mesotherm response group of Nix (1982), with mean annual temperatures in the 14–20°C range. No overview of the macrofossils is yet available to provide constraints on vegetation reconstruction, but there appear to be about 40 species of angiosperms and conifers including *Eucryphia* (Eucryphiaceae; Hill, 1991a), *Banksieaephyllum* (Proteaceae tribe Banksieae; Carpenter *et al.*, 1994b), *Gymnostoma* (Casuarinaceae; Scriven & Hill, 1995) and *Acmopyle* (Podocarpaceae; Hill & Carpenter, 1991). The evidence suggests that there was temperate rainforest here, more diverse than present Tasmanian rainforests, with gymnosperms forming the main canopy layer. The role of *Nothofagus* is unknown but it may have formed part of the canopy. There was a fairly diverse understorey of largely angiospermous shrubs (R.S.Hill, unpublished data; MacPhail *et al.*, 1994)).

The fossil woods are difficult to identify, except for some which are podocarpaceous, others related to Araucariaceae, and one possible *Nothofagus* (Taylor *et al.*, 1990). Structurally, most specimens show a wide zone of thin-walled early wood cells, terminated abruptly by a few thick-walled late wood cells, in what are markedly seasonal growth patterns. The annual rings are very narrow, with an average increment of something less than a millimetre, and consistency in width from year to year, all characters which suggest cool, rather uniform climates. There is no sign of frost damage. An essentially mild climate is suggested, with short winter days.

Virtually nothing is known of the structure of the vegetation, although it is reasonable to assume that this might have been controlled by high-latitude factors such as sun angle. From Cretaceous floras on the Antarctic Peninsula (see above) it is evident that the wide spacing of conical trees is a stratagem to maximise available solar radiation at such latitudes. This kind of evidence cautions against interpreting these Paleocene forests as closed forest communities. It is also probable that leaf arrangement in these forests was different to that found today in lower latitude areas, since Wells & Hill (1993) speculated that leaves may have tended to hang vertically to make better use of incoming light from the sun which was low in the sky. This would probably affect leaf size and shape and add a major difficulty to the utilisation of these characters in predicting prevailing climate.

While this was a highland vegetation, the pollen record suggests that lowland forests in the Gippsland Basin differed only in minor detail (Macphail *et al.*, 1994), so it seems there was little altitudinal zonation in Australia's south-east at this time.

Eocene

In the Eocene, in spite of its continued high-latitude position, Australia experienced considerable warmth (Feary *et al.*, 1991), and the early Eocene was probably warmer than at any other time in the Cainozoic. Fully marine conditions were established along the southern margin and a succession of high sea-levels flooded the coastal basins in south-western and southern Australia (BMR Palaeogeographic Group, 1990), in the west flooding old palaeovalleys almost as far north as Kalgoorlie. Each of these incursions carried its own suite of marine dinoflagellates (Harris, 1985; McGowran, 1989), which have provided a reasonably precise chronology.

Early Eocene: The palynological data suggest that the early Eocene in southern Australia was a period of major development of rainforests, which displayed some megatherm response characteristics (Macphail *et al.*, 1994). In extant terms, these are taxa which flourish under mean annual temperatures in excess of 24° Celsius and which are currently confined to the lowland tropics. It may be that the high moisture levels experienced at that time mitigated the seasonal effects that must have come with such high latitudes.

The megatherm character shows up in the diversity and dominance of angiosperms, which, in a most general way, contrasts with the Paleocene. *Nothofagus* species, however, were rare. In the coastal regions the megatherm character is seen in the most southerly expansion of mangroves, such as the palm *Nypa* and the fern *Acrostichum aureum*, which were associated in tidal wetlands as far south as Strahan in western Tasmania (Truswell, 1993).

Middle to Late Eocene: During the middle to late Eocene a cooling trend began that continued in a series of steps to the end of the Eocene. The general trend was interrupted with warmer phases, and these were related to the marine transgressions that crossed Australia's southern margins during the middle to late Eocene (see McGowran, 1989, for an overview).

Fossil floras are the most widespread of any phase of the Tertiary. The spread of sites ranges from oil shales in Queensland, through the south-east, into central Australia, across to the buried drainage channels in the western Australian shield. There are a number of key macrofossil floras, including those at Maslin Bay and Golden Grove, South Australia (Christophel & Blackburn, 1978; Christophel & Greenwood, 1987b; Scriven, 1993), Nerriga, New South Wales (Hill, 1978, 1980, 1982, 1986, 1989a) and Anglesea, Victoria.

Anglesea provides the best studied site, with both macrofossil and palynological data available together (Christophel *et al.*, 1987). Here, leaves and other macrofossils, including flowers and fruit, occur in a number of lenses in the sedimentary sequence. It is apparent that the local vegetation contributing to each lens was of a different character. The overall aspects of the assemblages suggested to Christophel *et al*. (1987) that the most instructive comparison was with living communities in lowland forest north of the Daintree River, Queensland, although the fruitlessness of trying to find precise analogues was acknowledged. The similarities rest on the abundant *Gymnostoma* remains in the assemblage, on fossil relatives of *Diospyros* and *Musgravea*, on numerous leaves of Lauraceae, Myrtaceae, *Brachychiton*, *Elaeocarpus*, Cunoniaceae, *Quintinia*, on *Podocarpus* and on the presence of rainforest cycads and ferns, including *Lygodium*. This kind of vegetation, with abundant broad-leaved, entire-margined angiosperms, occurs at all the known macrofossil sites except some in central and south-western Australia, but there are important floristic differences among the sites. In general, leaf physiognomy suggests mainly mesothermal vegetation, with perhaps some megathermal elements. There are probably numerous extinct species, and many leaves for which affinities remain unknown, but the links seem to be with low-latitude regions and not with present temperate vegetation.

The pollen record at Anglesea by and large mirrors the macrofossil, although there are some minor irregularities. The overall number of taxa is similar, and the major groups expected are all present in the pollen suites. But there are two major divergences: the pollen suites contain a much greater diversity of Proteaceae than the macrofossils do, and *Nothofagus* is well represented as pollen but unrecorded as macrofossils. *Nothofagus* pollen is present in frequencies up to 30%, and includes nine identifiable species in all subgenera, although subg. *Brassospora* species dominate. However, the difference in *Nothofagus* may be more apparent than real (see below), and a similar distinction in Proteaceae noted for Maslin Bay (Christophel & Blackburn, 1978), disappeared when the macroflora was examined in detail (Scriven, 1993).

This high representation of *Nothofagus* distinguishes all pollen floras of the interval. At about the early to middle Eocene boundary, across most of the sites in southern Australia, there is a marked increase in the representation of the genus. It applies to all subgenera, but particularly to subg. *Brassospora*, which may reach levels of 50–60% of the pollen spectra. Leaves of *Nothofagus* have not yet been generally reported from before the late Eocene (Hill, 1988; Pole, 1992), although Scriven *et al*. (1995) have reported a deciduous *Nothofagus* leaf from Maslin Bay and Carpenter & Pole (1995) have described dispersed cuticle of *Nothofagus* subg. *Lophozonia* from Lake Lefroy in Western Australia. It is not until the Oligocene that there are records of subg. *Brassospora* remains among the macrofossils (Hill, 1987, 1991b).

The conclusion to be drawn is that *Nothofagus* species may have been canopy dominants in areas away from the forest edges, and removed from the catchment areas for the macrofossils (Hill, 1990a) yet close enough to dominate the pollen suites. The ecophysiological studies provide a clue to this differentiation of habitat niches in that the living subg. *Brassospora* pollen producers appear to have a lower tolerance to temperature extremes and may have been less competitive in the exposed forest edges, whence most macrofossils come (Read *et al*., 1990). There may also have been other restricting factors such as soil character. However, no really satisfactory explanation has yet been suggested to account for the absence of *Nothofagus* subg. *Brassospora* parent plants among the macrofossil floras of the Early Tertiary, particularly as there was little topographic relief over much of the continent. It is worth noting some possible reasons why this absence may not be as significant as previously suggested. Firstly, the one *Nothofagus* leaf now reported from the extremely diverse Maslin Bay macroflora was deciduous, and thus not robust and unlikely to fossilise (Scriven *et al*., 1995). Maslin Bay is largely an impression flora, but where leaves are usually recovered as mummifications (e.g. Anglesea), deciduous leaves will not be found as they will not survive the chemical processing required. Secondly, Hill (1994a) noted that many leaves of *Nothofagus* subg. *Brassospora* are notophylls with entire or near entire margins. This is exactly the leaf type that dominates the mid-Eocene macrofloras and which have been targeted as being extremely difficult to identify. It is far too early to conclude that this subgenus is absent from these leaf floras. A single macrofossil site from the middle Eocene of central Australia (Christophel *et al*., 1992) suggests that provincialism was well-developed at this time, since it contains a more sclerophyllous vegetation than in the major contemporaneous floras from south-eastern Australia.

The pollen suites show marked regional differences in the Eocene. For instance, in the floras of coastal Queensland, *Nothofagus* is subordinate to Casuarinaceae, Araucariaceae and often Myrtaceae, a situation which contrasts with that in south-eastern Australia. It is in the minor elements of the pollen suites that key differences occur. In Queensland, taxa such as *Alyxia* (Apocynaceae), Arecaceae (including dicolpate pollen forms), Caesalpiniaceae, *Canthium* (Rubiaceae), and, commonly, Convolvulaceae are present. Many of these taxa are also found in the Murray Basin during the same time interval. Clearly, the vegetation of this wide marshy lowland had much more in common with that of Queensland than with that of the Gippsland and Bass Basins.

There is another suggestion of increasing provincialism at this time, when the palynological record from south-western Australia is examined. While most of the taxa at these sites are shared with those of eastern Australia (see Hos, 1975; Stover & Partridge, 1982; Milne, 1988), there are features that hint at the present strong endemism in the flora having a very long history. For instance, there is an extraordinary diversity of Proteaceae in the Eocene there; in sites near Zanthus individual pollen spectra have produced some 46 species of the family (Milne, 1988). The same spectra have also produced *Acacia* pollen, which is among the earliest records in Australia. A single macroflora from the region, which is unfortunately poorly dated, shows a great diversity of sclerophyllous Proteaceae and Myrtaceae, and bears little resemblance to macrofloras from the eastern seaboard (Hill & Merrifield, 1993). It has been concluded that this site demonstrates a sclerophyllous flora which had evolved in response to low nutrients. Later it was to be influenced by declining rainfall, at which time many of the conifers, *Nothofagus*, and *Gymnostoma* among others, became regionally extinct (Hill & Merrifield, 1993). Sclerophylly continued to increase at this time as well, and this is especially evident in the Proteaceae (Hill & Christophel, 1988). Other macrofloras are present in Western Australia (Carpenter & Pole, 1995; McLoughlin & Hill, 1996) and while they already offer support to the conclusions reached from the West Dale macroflora, further research is required on all these macrofloras to test existing hypotheses.

Early Oligocene to Middle Miocene

Continued northward migration of the continent occurred during this interval, with its northern margin reaching around 20°S (Veevers *et al*., 1991). There was a major fall in sea level in the middle of the Oligocene, associated with the buildup of Antarctic ice. Later, in the early Miocene, there were extensive incursions of shallow seas. These flooded the Eucla Basin, depositing the Nullarbor limestones; there was also extensive deposition of limestones and mudstones in the Murray Basin. In the Gippsland Basin peat accumulated in large freshwater swamps. Inland, there were extensive lakes and slow-moving rivers (BMR Palaeogeographic Group, 1990). Climatically, global temperatures continued to decline after the dramatic drops at the end of the Eocene. Broadly summarised, this was a time of global cooling, with major ice build-up on Antarctica, but there were local intervals of warmer excursions that are marked by marine transgressions in southern Australia.

There is a wealth of vegetation data but poor biostratigraphic control obscures its real significance. This was an interval of about 18 million years, with only a very limited number of rather uncertain subdivisions within it (Truswell, 1993). However, the fossil record preserves a variety of habitats and it is possible to identify some distinctive communities from the available evidence. For example, there were the lowland peat swamps of the Gippsland Basin, the highland floras of New South Wales and Tasmania, lowland, alluvial-fan deposits in Tasmania, and the enormous and complex riverine plain of the Murray Basin.

In the Oligocene there is the first extensive evidence for taxa having affinities with species growing in present-day high-latitude, cool-temperate rainforests. The influences of cooling in southern Australia can be seen in Tasmanian fossil sites such as at Pioneer, Cethana, Lemonthyme Creek, Little Rapid River and Lea River (Hill, 1983, 1987, 1990a, 1990b; Hill & Macphail 1983; Hill & Bigwood, 1987; Wells & Hill, 1989; Hill & Carpenter, 1991; Carpenter *et al*., 1994a; Scriven & Hill, 1996; Hill & Scriven, 1997). However, there are differences among these, so generalisations are difficult. The rich macrofossil floras contain a variety of *Nothofagus* remains including, at some sites, subg. *Brassospora* species, which were thus part of the nearby vegetation. One of the most interesting features of these floras is that they contain all four of the extant subgenera of *Nothofagus*, with three of them sometimes co-occurring in a single small catchment. These subgenera are currently separated by thousands of kilometres latitudinally (from the equator to about 40°S) and longitudinally from South America (where subg. *Nothofagus* is now endemic) to south-eastern Australia and New Zealand. This poses many important palaeoecological questions, the answers to which are still only partly understood. Another critical feature of the *Nothofagus* macrofossil record is that it provides insights into the evolution of the genus in response to climatic change. Leaf size changes, probably in response to cooling climates, have been recorded for the subg. *Lophozonia* (Hill, 1983, 1991b, 1994a) and subg. *Nothofagus* (Scriven & Hill, 1996), and interestingly the rate of response seems to have differed between the two. There is also important evidence of a much higher proportion of deciduous *Nothofagus* species in southern Australia than at present, where the only surviving deciduous species, *Nothofagus gunnii*, is now the only winter deciduous species in Australia. Finally, evidence from fossil cupules demonstrates that some of the extreme reduction common in subg. *Brassospora* in New Guinea (e.g. reduction of the number of fruits per cupule to one, and reduction of the two cupule valves to membranous flaps much smaller than the fruits) occurred in Tasmania in the Oligocene (Hill, 1994b), and thus cannot be considered as an adaptation to the extant New Guinea ecosystem.

There is also a range of conifers, including some taxa with descendants still in Tasmania (e.g. *Lagarostrobos*, *Athrotaxis* and *Phyllocladus* (Wells & Hill, 1989; Hill, 1989b; Hill *et al*., 1993), and also taxa that are now extinct in Australia, but which have near relatives on other southern land areas. These include the cupressaceous *Libocedrus* now restricted to New Zealand and New Caledonia, *Austrocedrus* and *Fitzroya* (South America), *Papuacedrus* (New Guinea), the podocarpaceous *Acmopyle* (New Caledonia and Fiji), and the more widespread *Dacrycarpus* and *Dacrydium* (Hill & Carpenter, 1989; Wells & Hill, 1989; Hill & Whang, 1996). Extinct genera of podocarps have also been described (Hill & Pole, 1992). The presence of these taxa cautions against trying to find living analogues for these Tertiary communities.

Trends in leaf size and stomatal distribution thought to be linked to climate change have also been described in some conifer genera. In particular, *Dacrycarpus* decreased its leaf area by reducing the amount of bilaterally flattened foliage and reduced the stomata on the bifacially flattened foliage, eventually losing them altogether from the abaxial surface. *Acmopyle* appears to have been unable to modify its leaf area, but was able to reduce its stomatal distribution by producing hypoplastic stomata on the functional upper surface of the bilaterally flattened foliage (Hill & Carpenter, 1991).

The pollen floras of this period are dominated by *Nothofagus*, mainly subg. *Brassospora*, but they show a diversity of other species, and a varied angiosperm flora, as well as the conifers. In essence, there is a mix of plants with relatives that now are geographically widespread; they have a latitudinal and an altitudinal spread that ranges from low altitude forests at low latitudes, to high altitudes at high latitudes. Hill (1990a) has grouped the taxa into those with affinities to taxa growing today only at low latitudes, including a number of conifer species, *Gymnostoma*, Lauraceae and *Nothofagus* subg. *Brassospora*; those which have migrated north but left descendants in the south, such as *Nothofagus cunninghamii*; those which occur now at mid-latitudes on Australia's east coast, for example *Nothofagus moorei* and *Eucryphia moorei*; and those taxa which have remained in the south, of which *Nothofagus gunnii*, *Phyllocladus*, *Athrotaxis* and *Microstrobos* are examples. There are also a number of extinct taxa within the fossil floras with no extant descendants. The evolution of the living forest types can be viewed as a sifting of these Oligocene 'mixed' forests over very long periods of time, in response to climatic change, or to a complex of selection pressures. One of these sifting mechanisms may have involved the replacement of forest dominants by recruitment from the relatively unstable habitats at the forest margins.

Evidence for the presence of open heath-like communities comes from the lowland peat swamps of the Gippsland Basin. Regional pollen assemblages are typical for the time in being dominated by *Nothofagus*, but there are particular pollen suites in which Epacridaceae and Gleicheniaceae are common, with high *Banksia* and Restionaceae counts (Luly *et al.*, 1980). In the Yallourn Seam, which is probably mid-Miocene in age, there is a high content of fusinite or fossil charcoal, and the macrofossil suite is dominated by Gleicheniaceae and Typhaceae. Blackburn & Sluiter (1994) have suggested that these were reedy swamps growing under seasonally dry conditions and controlled by a natural fire regime (Fig. 68). *Banksia* remains are widespread in sediments as old as perhaps middle Eocene (McNamara & Scott, 1983), and Hill (1990a, 1994a) has suggested that fossils of this genus may provide evidence of the pathway by which the sclerophyllous heath flora evolved. Most leaves of the early taxa show little evidence for the protection of stomata from drying out, and may thus indicate that sclerophylly arose initially not in response to climate change but as an adaptation to edaphic factors; they were thus pre-adapted to the pressures of aridity in the later Cainozoic. However, the recent description of leaves from the Late Paleocene Lake Bungarby flora (Carpenter *et al.*, 1994b), which look very much like some extant Western Australian *Banksia* species, may change that interpretation. An explanation of the early evolution of scleromorphic taxa remains one of the great challenges to macrofossil palaeobotany in Australia.

The development of another vegetation type can be seen in the Murray Basin. A great variety of habitats is preserved there but, as elsewhere, floras tend to be dominated by *Nothofagus*, or by Casuarinaceae and gymnosperms. There are common halophytes (Chenopodiaceae for instance) and there is the best record in Australia of *Acacia*, which has an essentially continuous presence since the early Oligocene (Truswell, 1993).

Two points of major importance arise from the Murray Basin record. The first is that the sheer richness of species is much greater than that of contemporary floras in the Gippsland Basin and Tasmania, and no doubt reflects the diversity of habitats. The second point is that in this basin there is a clear palynological shift away from dominance by *Nothofagus* to dominance by Myrtaceae and Casuarinaceae, through a phase in which Araucariaceae are prominent. This shift happened in the late Oligocene to early Miocene, and is evident in pollen counts from a number of boreholes in the basin (Macphail & Truswell, 1989). Locally at least, it appears to have been time transgressive. Little is known about the early history of this drier style of rainforest, which has a notable presence of *Araucaria* and high Myrtaceae and podocarp frequencies. It could have expanded from dry areas in the centre of the continent, or could be a new association that developed with mid-Tertiary seasonal dryness. Apart from moving coastwards in the south-east, it also moved north, and is known from the north-east where there are records from the Pliocene and Quaternary, particularly during glacial maxima. Kershaw *et al.* (1994) have shown this spread diagrammatically. Fig. 69 shows how the proportions of 'dry' and 'wet' rainforest types varied geographically from the Miocene to the Quaternary, from the earliest known occurrence in the Murray Basin.

One special feature of this time period is that it marks the first reasonably widespread occurrence of *Eucalyptus s. lat.* macrofossils in Australia. *Eucalyptus s. lat.* has justifiably been called the 'universal Australian' (Pryor & Johnson, 1981). The group currently contains more than 700 taxa, which are nearly all endemic to Australia. Lange (1980) noted that eucalypts have been estimated to contribute 75% of the extant Australian vegetation, and at the wetter margins of the continent they dominate nearly all vegetation except rainforest and allied mesic types. Only in the arid Australian interior are eucalypts not dominant. Thus it is especially instructive to examine the fossil record of the eucalypts in some detail. In this discussion *Eucalyptus* is treated for convenience in its broad sense, rather than as *Eucalyptus s. str.*, *Angophora* and *Corymbia* (Hill & Johnson, 1995).

Eucalyptus is both highly diversified (Johnson, 1972; Pryor & Johnson, 1981) and dominant in many communities, it would therefore be expected to yield a complex and challenging fossil record. While this is not the case (Lange, 1978b, 1980, 1982), *Eucalyptus* does have a macrofossil record that is more detailed than is usually acknowledged (Hill, 1994a). While Maiden (1922) gave descriptions of 19 macrofossil *Eucalyptus* species, as well as four records of subfossils which were assigned to extant species, some later authors apparently ignored this in commenting on the almost total absence of the genus from the macrofossil

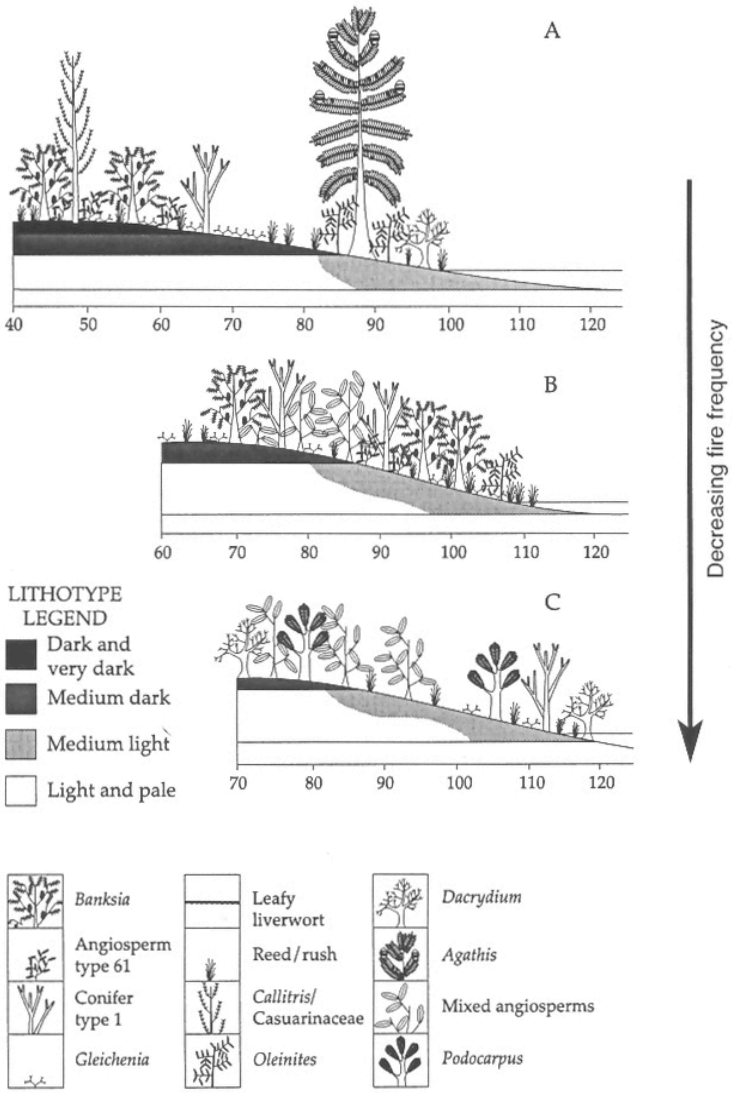

Figure 68. Hydroseral and pyric succession for three intervals from the Yallourn Open Cut. Water levels indicate probable permanent inundation. **A.** Succession under the influence of frequent fires. The margins of open water are essentially a *Dacrydium*-*Oleinites*-*Agathis*-reed/rush swamp. On drier areas above this is a reed/rush-*Gleichenia* moor. This grades into a *Banksia*-*Gleichenia*-conifer-reed/rush scrub. Rare *Callitris* and Casuarinaceae occur on the driest parts with leafy liverworts. **B.** Succession under the influence of infrequent fires. The margins of open water are occupied by an *Oleinites*-*Gleichenia*-reed/rush swamp. On the drier areas above this is a *Banksia*-*Gleichenia*-angiosperm-conifer scrub. Above this again is a region having a mixed angiosperm scrub. On the driest parts *Banksia*-*Gleichenia*-reed/rush scrub dominates. **C.** Succession under the influence of very infrequent fires. The margins of the open water are colonised by a *Dacrydium*-*Gleichenia*-conifer-reed/rush swamp. On the drier areas there is a mixed angiosperm-*Podocarpus*-*Dacrydium* scrub. Conifer type 1 and angiosperm type 61 represent currently unidentified macrofossil taxa. Modified from Blackburn & Sluiter (1994).

record (Lange, 1980; Christophel, 1989). Hill (1994a) comments on possible reasons for this change in attitude towards the macrofossil record.

The oldest reliably dated and described macrofossil associated with *Eucalyptus* currently reported is a tree stump which is probably *in situ*, and which is enclosed in a 21 Ma old basalt in the upper Lachlan Valley of New South Wales. The wood is reasonably well-preserved and has been identified by Bishop & Bamber (1985) as 'Myrtaceae with affinities to *Eucalyptus* B' (of Dadswell, 1972), although confirmation of this by identification of diffuse parenchyma cells was not possible. Holmes *et al*. (1982) described *Eucalyptus bugaldiensis* from the middle Miocene Chalk Mountain Formation in the Warrumbungle Mountains of New South Wales, based on impressions of umbel-shaped infructescences. They also described two *Eucalyptus* leaf types from impressions, noting that at least two of the phylogenetic lines proposed by Johnson (1972) for *Eucalyptus* were present at the site. They concluded that the fossils exhibited some features of advanced states in both fruits and leaf venation.

Deane (1902) described seven species of *Eucalyptus* from middle Miocene sediments at Berwick in Victoria, and Holmes *et al*. (1982) noted the presence of a leaf with *Eucalyptus*-like cuticle and an impression of a eucalypt-like fruit in the flora. This site was extensively re-collected by Pole *et al*. (1993), and several leaves with reasonably well-preserved cuticle were recovered that have clear affinities with *Eucalyptus*. *Eucalyptus* macrofossils have also been recovered recently from Miocene sediments in northern New South Wales (R.S.Hill, unpublished data) and there are also Pliocene leaves named *E. pluti* from Daylesford in Victoria (McCoy, 1876). McCoy noted that these leaves are almost identical in size and shape to extant *E. globulus*, but he noted some minor differences in the venation pattern.

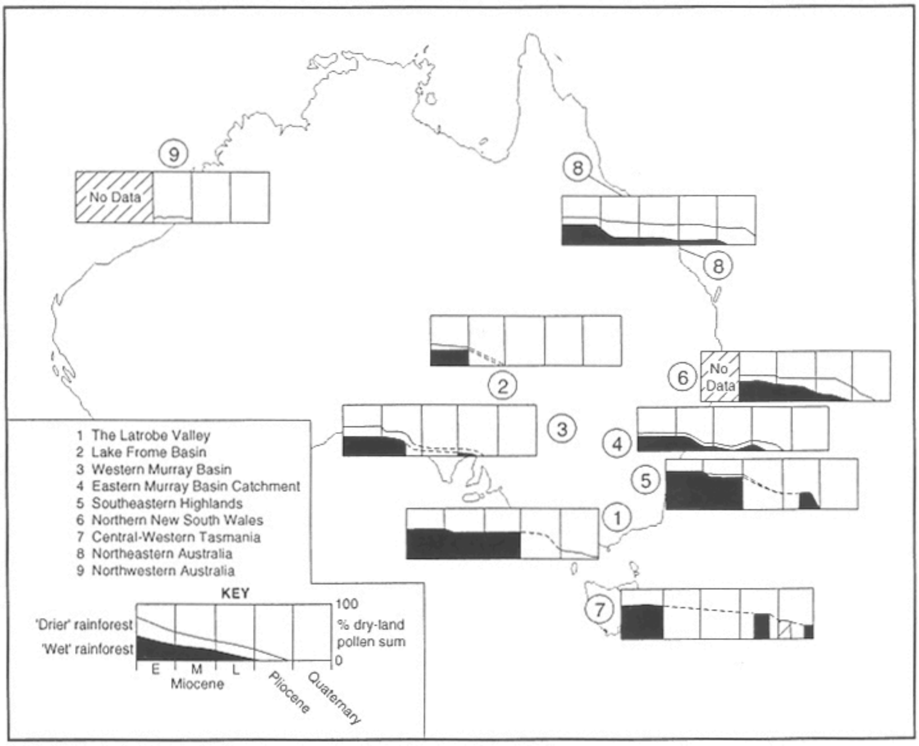

Figure 69. The Neogene pattern of rainforest decline. Modified from Kershaw *et al*. (1994).

The macrofossil record of *Eucalyptus* from central Australia is very important but frustratingly uncertain. Lange (1978b) described several excellent casts of eucalypt-like fruits, which are only part of a more diverse collection from Island Lagoon, near Woomera. Unfortunately, there is poor age control on this diverse assemblage of eucalypts, which may be either Eocene-Oligocene or Miocene in age (Ambrose *et al*., 1979). Greenwood (1991) reported 'the earliest record' of *Eucalyptus* macrofossils from the middle Eocene silcretes in the Eyre Formation in central Australia, but he neither described nor illustrated these macrofossils, and in his earlier work on the flora (Greenwood *et al*., 1990) he only mentioned leaves assigned to *'Eucalyptophyllum'*, about which he concludes 'it is not possible to determine the affinities of this leaf type'. If unequivocal *Eucalyptus* fossils have been found in middle Eocene sediments in central Australia, their formal description should be a high priority.

Eucalyptus macrofossils are absent from several near-coastal south-eastern Australian Paleocene to Early Oligocene floras. It is also notable that *Eucalyptus* has not been reported from the Latrobe Valley coal macroflora (Blackburn & Sluiter, 1994). Allied to this is the argument presented by Archer *et al*. (1991) that the relative rarity of early koalas in Oligo-Miocene rainforests may have been due to the rarity of eucalypts in that vegetation.

Current evidence, sparse as it is, favours the hypothesis of Lange (1980) that in the mid-Tertiary the continental margins of Australia supported only mesic non-eucalypt vegetation, while eucalypts contributed to the more xeric vegetation in the interior. With progressive development of central Australian aridity, it is likely eucalypts were displaced to the continental margins while most mesic vegetation was eliminated altogether. It is informative that the late Oligocene-Miocene coastal sites where *Eucalyptus* has been recorded do seem to contain rainforest vegetation which is less mesomorphic in character and may represent a transition to drier climate forest (Hill, 1994a).

The early pollen record of *Eucalyptus* is even more enigmatic than the macrofossil record, partly because fossil pollen which has sometimes been referred to *Eucalyptus* is also similar to *Angophora, Syncarpia* and possibly *Metrosideros* (Martin, 1978). Cookson & Pike (1954) described *Myrtaceidites eucalyptoides* for pollen grains with probable affinities with *Eucalyptus* and noted its range as Pliocene to Pleistocene. However, this pollen type, which is referred to as the *Angophora*/*Corymbia*-type of pollen (Martin, 1989, 1994) is now recorded from the Late Paleocene of the Lake Eyre Basin in inland Australia. Harris (1965) described *Myrtaceidites tenuis,* and noted that this species is a very rare form, similar to forms related to *Eucalyptus* by Cookson & Pike (1954). *Myrtaceidites tenuis* does not persist beyond the Eocene, and its possible affinity with *Eucalyptus* is particularly interesting, since the eucalypt-type does not appear again in south-eastern Australia until well into the Oligocene (Hill, 1994a).

In more recent sediments, there is excellent evidence for a dramatic increase in abundance of *Eucalyptus* associated with increased charcoal levels. Although this occurs at different times in different parts of Australia, this is compelling evidence for the influence of Aborigines in artificially increasing the fire frequency (Singh *et al*., 1980; Kershaw, 1986). Thus the current superdominance of *Eucalyptus* in Australia may be a relatively recent phenomenon, the result of the extraordinary adaptation of the genus to fire (Jackson, 1968) coupled with an artificial increase in ignition associated with the arrival of Aborigines. A drying climate probably assisted this event, since the vegetation was then much more prone to burn once it was lit (see Flannery, 1994, for a detailed discussion of the effect of Aborigines on the vegetation).

An important aspect of the *Eucalyptus* fossil record is its apparent presence in both South America and New Zealand. Frenguelli (1953) described *Eucalyptus patagonica* from a group of three fruits in Miocene (now considered to be probably Eocene, E.J.Romero, pers. comm.) sediments in Patagonia. Johnson & Briggs (1984) discussed this fossil and others which had been collected since, noting that Frenguelli's specimen 'could conceivably belong among the more generalised members of *Symphyomyrtus*', but they did not consider that the other specimens they saw belonged to the *Eucalyptus* alliance. Future research on these fossils will be particularly important to those with an interest in the origin and evolution of *Eucalyptus*.

Pole (1989) described leaves from Early Miocene sediments in the South Island of New Zealand which are 'identical to many *Eucalyptus* species', and noted their occurrence with eucalypt-like fructifications. This record is far more reliable than that from South America, especially when it is considered in conjunction with the pollen record. Mildenhall (1980) lists the stratigraphic range of *Eucalyptus* pollen in New Zealand as Miocene-Early Pleistocene, suggesting a relatively recent extinction.

These extra-Australian records are of great significance in tracing the history of the genus. The New Zealand records either represent long distance dispersal from Australia, in the Miocene or earlier, or they represent part of an ancient lineage which was present across at least part of Gondwana prior to separation of New Zealand and Australia, but which did not assume prominence (and thus appear in the fossil record) until climatic changes favoured its expansion (Hill, 1994a). It is impossible to decide between these options at present, although long-distance dispersal is now being invoked for *Nothofagus* from Australia to New Zealand (Martin & Dowd, 1993; Macphail *et al*., 1994; Hill *et al*., 1996) and perhaps for much more of the flora (Pole, 1994), but for *Eucalyptus* the South American record will prove crucial. If further work confirms a link between the South American fossils and *Eucalyptus*, then an ancient (Cretaceous?) Gondwanic distribution for this now characteristically Australian genus would have to be considered the most likely hypothesis (Hill, 1994a).

Latest Miocene to Pliocene

This interval is best dealt with as a single unit, because of the difficulties of separating late Miocene from early Pliocene deposits. The best evidence for trends in the vegetation comes from sequences in the river valleys draining westward from the Dividing Range; the Lachlan Valley preserves the most continuous record.

We see there, some time in the late Miocene, a marked decline in the abundance of *Nothofagus* in the pollen spectra; indeed there is a complete elimination of subg.

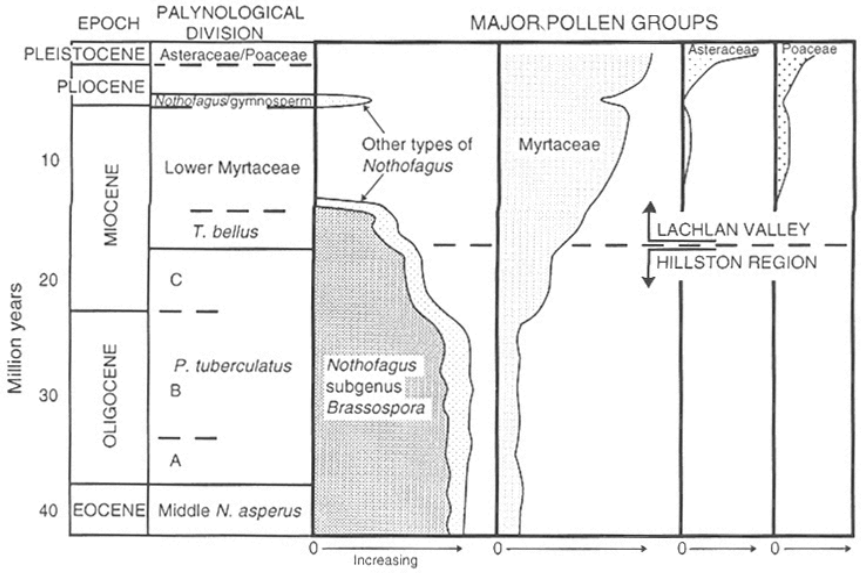

Figure 70. Major pollen groups for the late Miocene-Pliocene in the Lachlan region, northern New South Wales. Modified from Martin (1991) and Truswell (1993). *T. bellus* = *Triporopollenites bellus*; *P. tuberculatus* = *Proteacidites tuberculatus*; *N. asperus* = *Nothofagidites asperus.*

Brassospora and a corresponding increase in Myrtaceae (Fig. 70). The nature of this surge in Myrtaceae, which Martin (1987, 1991) called the 'Lower Myrtaceae phase' is problematic in terms of the vegetation it represents. Some of the increase in abundance represents eucalypts but other, more rainforest-related taxa are present too, including pollen that Martin assigned to *Tristania*, *Syzygium* and *Backhousia*. These now occur in wet sclerophyll forests. Here again there is evidence of fire (Fig. 71). Charcoal counts increase dramatically, probably under conditions of reduced precipitation and more seasonal rain. These communities seem to have been subject to more burning than phases that were clearly rainforest. This may strengthen the claim that this Myrtaceae phase reflects wet sclerophyll communities, possibly with a myrtaceous canopy above an understorey containing some rainforest taxa, and akin to communities bordering rainforests in northern Queensland today.

In the Pliocene, probably at different times according to geographic location, the trend from closed forests to open vegetation seems to have accelerated (Fig. 72), probably in response to climatic swings which were comparable to those of the Pleistocene. There are hints of savanna vegetation in north-western Australia. In pollen spectra from the Ocean Drilling Program site off the north-west margin there is substantial grass pollen at the beginning of the Pliocene (Kershaw *et al.*, 1994), but we know little of the associated trees.

At Lake George near Canberra the record is better, but there are big gaps. Dating there has been by magnetic reversal stratigraphy (McEwen Mason, 1991). The sequence shows a fairly

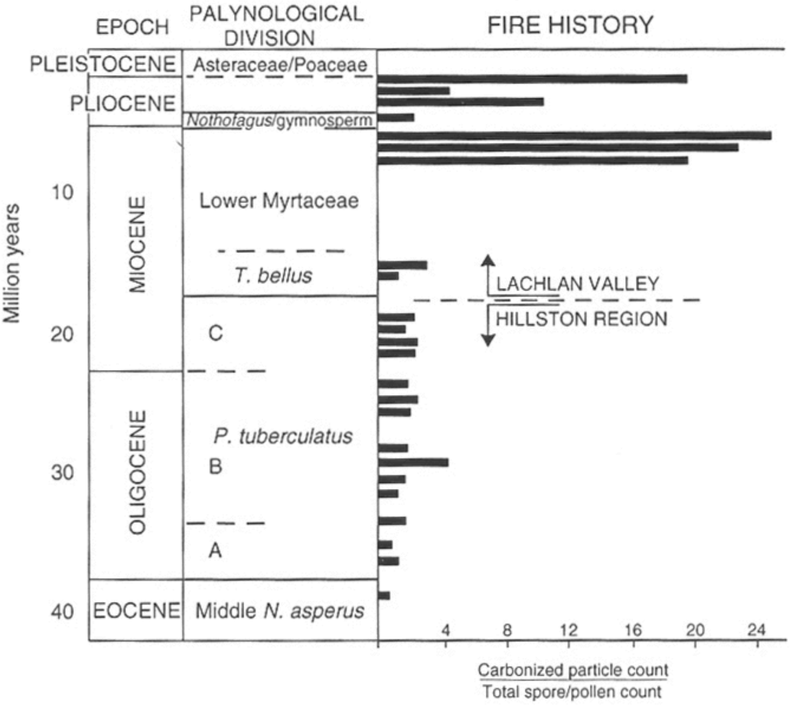

Figure 71. Suggested vegetation types represented by pollen spectra in the Lachlan region. Carbonised-particle content reflects changes in the fire history. Modified from Martin (1991) and Truswell (1993). *T. bellus = Triporopollenites bellus*; *P. tuberculatus = Proteacidites tuberculatus*; *N. asperus = Nothofagidites asperus.*

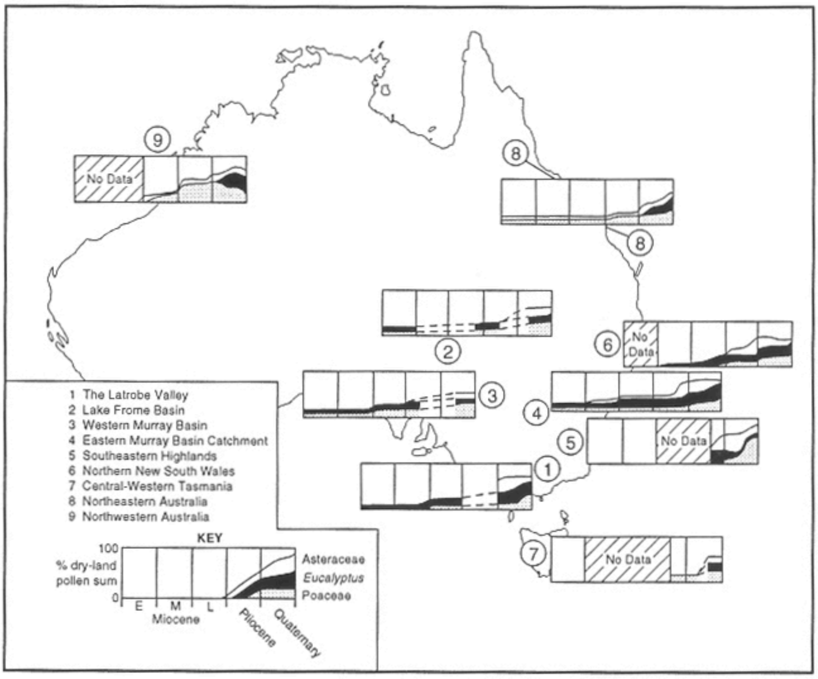

Figure 72. The Neogene increase in selected components of open vegetation. Modified from Kershaw *et al*. (1994).

dramatic shift in the late Pliocene from what seems to be temperate rainforest with *Nothofagus*, Podocarpaceae and some *Araucaria*, to a dominance by Asteraceae and grasses, in a landscape with very few trees. The Asteraceae pollen is mainly referable to the fossil species *Tubulifloridites pleistocenicus*, which is common in the Pleistocene but whose affinity is unknown (Macphail & Martin, 1991). The nature of this open vegetation remains problematic, as do the climatic conditions it reflects. Speculatively, conditions may have been cool and dry; they may reflect the first winter rainfall communities within this region.

Quaternary

The pollen record for the Quaternary consists mainly of extant Australian taxa, with a few exceptions, but there is a great deal of evidence for shifts in species' ranges and associations as glacial cycles progressed. There is certainly abundant palynological evidence for fluidity of plant communities during this time. However, the scant macrofossil evidence suggests that, in the Early Pleistocene at least, there were still many species present that are now extinct, and the glacial cycles must have been extremely important in sifting communities, especially at high latitudes (Hill & Macphail, 1985; Macphail *et al.*, 1993; Jordan, 1994, 1995; Jordan & Hill, 1994).

The Australian vegetation has been altered enormously in more recent time since the arrival of first Aboriginal and later European people. The detail of that change, which is largely the result of land clearance by fire and for agriculture has been summarised recently by Kershaw (1988), Flannery (1994) and Hope (1994).

Summary of Cainozoic vegetation

In summary, the record that we have now, in spite of its limitations, and its bias towards wet habitats and data from south-eastern Australia, gives a general picture of a transition from widespread, very diverse and complex-patterned rainforests, to predominantly open vegetation with rainforest restricted to wetter regions. There are aspects of the early Tertiary forests that we have not yet explored sufficiently. The constraints that the high latitude position must have placed on these are one such issue: in attempting to reconstruct these forests we may have been overly influenced by apparent similarities with present low-latitude vegetation.

The rainforest elements identifiable in the early Tertiary are now segregated along a latitudinal gradient in eastern Australia. The processes of change to cooler, more seasonal conditions are still elusive, but morphological changes are apparent in a number of important lineages (e.g. in conifers and *Nothofagus*). This process of opening out may go back a long way; *Banksia* in the Paleocene and Eocene may record the development of sclerophylly at that time, and *Acacia* is now known nearly as far back and was well-established in the Oligocene, but is unknown as macrofossils in pre-Quaternary sediments.

We know that by at least the mid-Miocene there was heath-like vegetation established locally in coal swamps and growing under particular fire regimes. The drier rainforests, with abundant *Araucaria*, seem to have been established first at inland localities, perhaps because *Nothofagus* subg. *Brassospora* could not compete effectively under more seasonal rainfall. We know little of the origins and structure of these forests.

There is evidence that fire was important in developing other communities in the Tertiary, perhaps including wet sclerophyll forests. These have been identified in the late Miocene, linked with increases in the quantity of charcoal in sediments. Grassland and savanna seem to have become established in the Pliocene, but their histories are sketchy and there are no data from northern Australia that can be linked in a continuous way with modern savanna vegetation. There is so far no recognised modern analogue for the enigmatic Pliocene and Pleistocene daisy-rich vegetation. The massive expansion of the eucalypts, probably at the expense of the drier rainforests and Casuarinaceae woodlands, is a more recent story and has possible links with human land-management practices, although there was apparently a much earlier shift of eucalypts from central to coastal Australia.

On the broader issues of phytogeography, there is sufficient evidence now to suggest that much of the present Australian vegetation is of Gondwanan stock. The record does, however, suggest that some interchange occurred with regions to the north during the Cretaceous and Tertiary. We cannot yet see any evidence for large scale invasions in the Miocene. The developing record from Antarctica indicates that this area formed a dispersal centre and migration route for many taxa which now have disjunct distributions in middle or low latitudes.

There are major gaps in our knowledge. We have far too little information, from either pollen or macrofossils, about Australia's north. There are very large numbers of macrofossils, mainly leaves, whose affinities remain unknown. But it is the present strength and the potential of the fossil record that leaves an impression. There will be major advances in Australian palaeobotany in the future, and for the first time there is a concentrated effort to frame questions in advance of the research. This will lead to major breakthroughs in our understanding of the history of the vegetation and provide a thorough framework for those researchers who base their work on the living flora.

Acknowledgments

Our thanks to Roger Buick and Malcolm Walter for discussion on the Australian Precambrian. The Australian Research Council has funded the research of three of the authors (RSH, SMcL and MED) for many years.

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BIOGEOGRAPHY OF THE TERRESTRIAL FLORA

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Taxonomists usually map distributions of plants in their monographs and flora treatments, and they have always been intrigued by the resulting patterns. This has led them to pose questions such as 'Why do related taxa occur in widely disjunct areas while unrelated taxa share similar, endemic distributions?', and 'What were the geological, climatic and biological causes of such patterns?' Biogeography is the science of analysing and explaining biotic distributions. It is a 'big picture' science because it requires knowledge of taxonomy, evolution, ecology, palaeontology, geography, geology and climate. Or, as Croizat (1962) put it, biogeography is the integration of evolution through space, time and form.

Biogeographers look to the earth and its processes, such as plate tectonics and climate change, as the driving forces behind distributional patterns. Furthermore, many workers have been tempted to 'fit' biotic patterns to geological and climatic hypotheses. For example, the advent of continental drift theory stimulated research in biogeography (Raven & Axelrod, 1974; Axelrod & Raven, 1982; Briggs, 1987; Whitmore, 1987). However, there is no need to give primacy of explanation to earth processes (Ball, 1976). Biogeographic hypotheses can be formulated in the absence of any process explanation and moreover, they should be, to avoid circularity in later using biogeographic patterns to test process hypotheses. Indeed, the evidence of biotic distributions, past and present, strongly influenced geologists to accept the theory of continental drift (Tarling, 1980; White, 1986). This primacy of pattern over process is a general principle of comparative biology (Cracraft, 1989; Humphries, 1988; Eldredge & Cracraft, 1980; Sluys, 1994).

Description, narration and analysis

Ball (1976) suggested that all studies of historical biogeography pass through three phases: descriptive, narrative and analytical. The descriptive phase is the discovery of intriguing biotic distribution patterns as a result of routine taxonomic practice. It includes patterns of individual taxa and compilations of multiple taxa and whole biotas. The latter are expressed as maps of biotic regions which are characterised by high endemism. Such maps have been produced at various scales, e.g. the world (Wallace, 1876; Sclater & Sclater, 1899; Good, 1974; Takhtajan, 1986), regional (Van Steenis, 1963; Van Steenis & Van Balgooy, 1966; Van Balgooy, 1975, 1984, 1993) and national. National maps for Australia have been produced by, among others, Spencer (1896), Burbidge (1960) and Schodde (1989); see Figs 73 & 74.

Narrative biogeography attempts to explain the historical causes of observed distributions by constructing a scenario with a series of unique events that affected a particular taxon. For example, Schodde (1972) hypothesised that the angiosperm family Pittosporaceae originated in the Australian or Indian Ocean region, then migrated outwards to the Pacific, Africa and Asia as it diversified. Few biogeographic studies progress beyond this phase. While these scenarios may be valuable in ordering and collating information about the taxa on which they are based, narrative biogeography lacks predictive power and has little application to development of more general explanations of distribution (Ball, 1976).

The analytical phase of biogeography (Ball, 1976) formulates testable hypotheses. These are general explanations usually involving multiple taxa and so may be corroborated by new evidence from previously uninvestigated organisms or taxa. For example, Lyne (1993) made a bioclimatic analysis of the rare species *Leptospermum namadgiensis* (Myrtaceae), which is restricted to the Australian Capital Territory/New South Wales border ranges. This analysis predicted new occurrences on mountain peaks not previously explored, and the species was subsequently found there. Analytical methods include the equilibrium theory of island biogeography (McArthur & Wilson, 1967), bioclimatic analysis (Nix, 1982), and cladistic biogeography (Nelson & Platnick, 1981; Humphries & Parenti, 1986). Croizat's panbiogeography (Croizat, 1952, 1958, 1962) falls somewhere between narrative and analytical methods (Ball, 1976; Craw & Weston, 1984).

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Rosen (1988) argued that processes hypothesised to explain distributional patterns form a continuum over time and geographic scale. He organised these into three overlapping groups: *maintenance*, representing current or recent processes which maintain the presence of a taxon in a given area, and those processes that exclude it from other areas; *distributional change*, representing changing environments and responses by organisms such as adaptation, dispersal, range-contraction and range-expansion; and *origination*, being long-term evolutionary change such as speciation and extinction, often in relation to major earth events.

Research programs of ecological and historical biogeography may be differentiated in relation to Rosen's classification. Maintenance is concerned with short-term processes operating on a scale of thousands of years and is the sole domain of ecological biogeography. Origination concerns very long time scales of millions of years, and is the sole domain of historical biogeography. Both programs overlap in the middle of the scale (distributional change). For example, analyses of the monsoon tropical flora of northern Australia and New Guinea by Nix & Kalma (1972) and Crisp *et al.* (1995) both made predictive inferences about the causes of the floristic similarity of these areas. However, Nix's method was concerned with climate and belongs to the domain of ecological biogeography, whereas Crisp *et al.* were concerned with cladistic methods from the domain of historical biogeography.

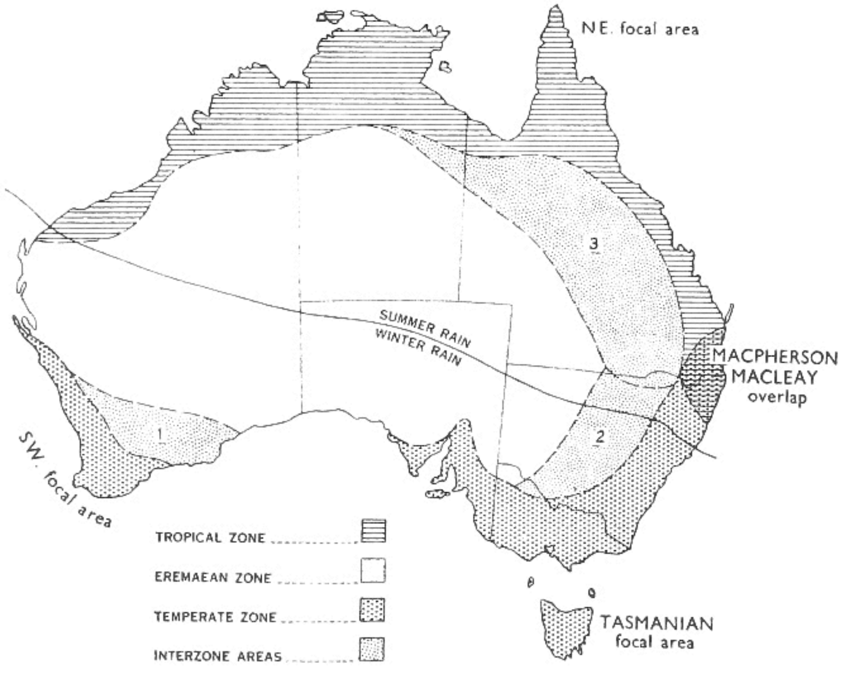

Figure 73. Map of floristic zones (equivalent to biotic regions or elements) in Australia. Reproduced from N.Burbidge, *Austral. J. Bot.* 8: 79 (1960) with permission.

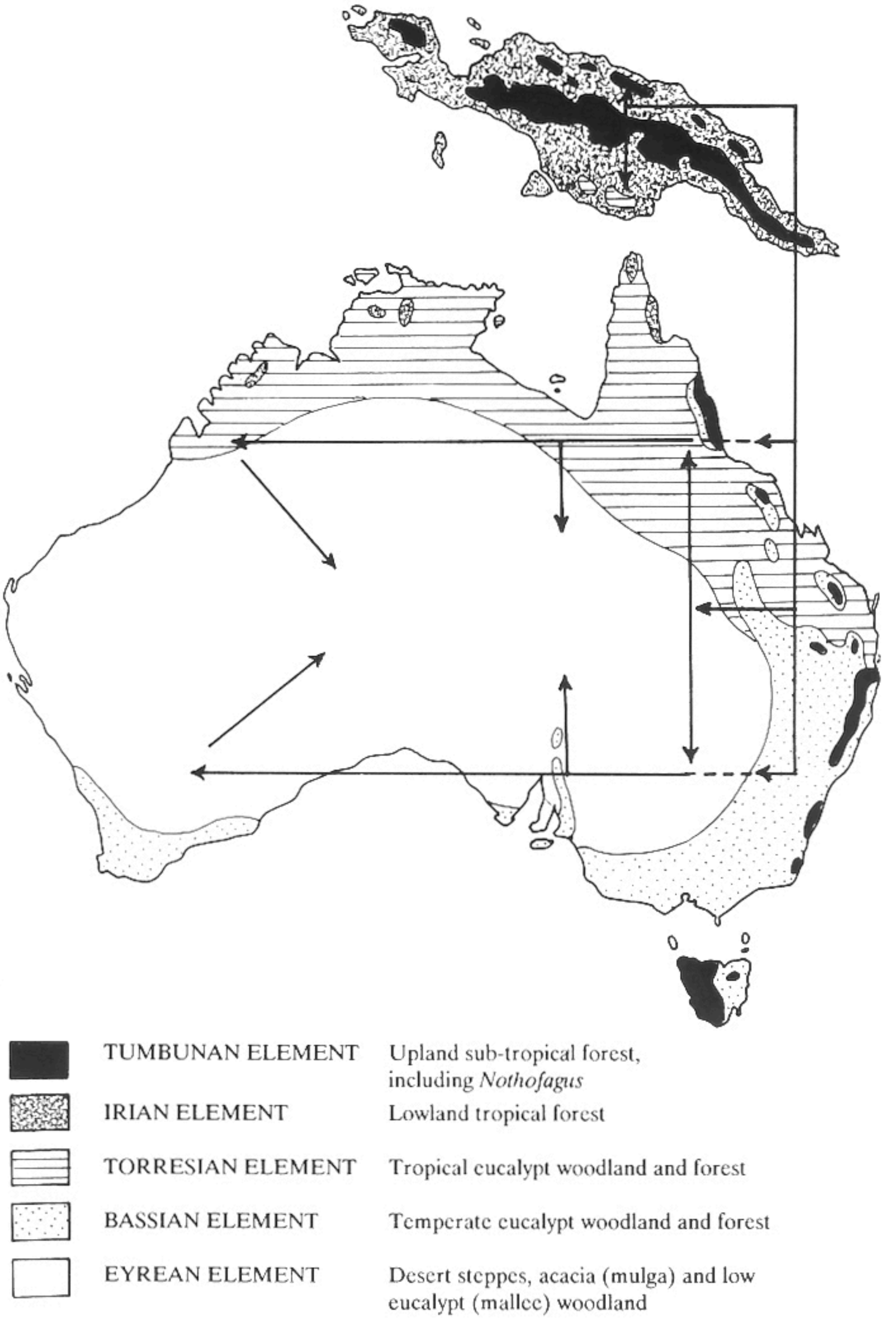
TUMBUNAN ELEMENT
Upland sub-tropical forest, including *Nothofagus*
IRIAN ELEMENT
Lowland tropical forest
TORRESIAN ELEMENT
Tropical eucalypt woodland and forest
BASSIAN ELEMENT
Temperate eucalypt woodland and forest
EYREAN ELEMENT
Desert steppes, acacia (mulga) and low eucalypt (mallee) woodland

Figure 74. Map of biotic elements in Australia and New Guinea. This map is based on that of Burbidge (Fig. 73), but recognises additionally the Tumbunan and Irian elements. Arrows indicate putative pathways of migration and radiation. Reproduced from R.Schodde, Origins radiations and sifting in the Australasian biota - changing concepts from new data and old, *Austral. Syst. Bot. Soc. Newsletter* 60: 10 (1989) with permission.

Furthermore, different elements of the same biota may have different histories which are the outcomes of different processes. Thus, a Livistona fan palm which is endemic to a central Australian gorge might be growing next to a cosmopolitan Phragmites reed. The nearest relative of the fan palm may be a species occurring in distant gorges of the Great Dividing Range in eastern Queensland. These two species of Livistona may be descended from a common ancestor dating back to the Miocene, when perennial rivers and freshwater lakes made a continuous link from central Australia to eastern Queensland. The ancestor may have spread widely across this river system, rather as the more hardy river red gum does today over these same but now intermittent watercourses. As aridity set in through the Pliocene, the rivers and lakes dried up, and the distribution of the ancestral fan palm shrank to refuges along perennial billabongs in the central Australian ranges and the Great Dividing Range. With a vast distance separating them, these now vicariant populations could have evolved into distinct species. This history of ancient speciation by vicariance (splitting of an ancestral range) can be reconstructed today by overlaying a phylogeny of Livistona on a map of the distributions of the species. If other taxa endemic in the same areas, such as Macrozamia cycads, show the same phylogenetic relationship between areas, then the hypothesis of vicariance is corroborated.

On the other hand, the *Phragmites* is a single species spread widely in wetlands thoughout Australia and beyond, even as far away as Africa. Unsuitable desert habitats and even oceans seem to provide no barrier to the dispersal of its seeds, which are easily blown on the wind. This may be a ‘young’ species that has spread quickly around the world. Thus vicariance may not affect it, and its distribution would be best explained by climatic or ecological modelling, assuming that its dispersal has not been historically limited. Further research is needed before we understand the limits of applicability of ecological and phylogenetic methods, especially for events of intermediate age, e.g. Pleistocene.

Hereafter this chapter is concerned primarily with historical biogeography, that is ancient patterns of the kind shown by *Livistona*. Australian ecological biogeography is discussed further in the present volume by Groves (*q.v.*).

History of biogeographic studies on the Australian flora

J.D. Hooker and his legacy

Study of the phytogeography of the Southern Hemisphere, including Australia, effectively began with Joseph Hooker (Brundin, 1966). His was the earliest attempt at a consolidated description of the composition and affinities of the Australian flora. Hooker visited Australia, New Zealand, Patagonia and various sub-Antarctic islands during 1839–1843 as Assistant Surgeon with James Clark Ross' *Erebus* and *Terror* expedition. During and shortly after this voyage, Hooker was struck by the close affinities, especially at generic level, between the southern lands, despite their separation by vast tracts of ocean. He came to the conclusion that he had discovered a circumpolar Antarctic flora, and that the present-day floras had evolved, at least in part, by the development of physical and climatic barriers between formerly contiguous areas (letter to Darwin of 1 September 1845, cited in Anonymous, 1997). In *Flora Novae-Zelandiae* (Hooker, 1853) he stated:

> '*Enough is here given to show that many of the peculiarities of each of the three great areas of land in the southern latitudes are representative ones, effecting a botanical relationship as strong as that which prevails throughout the lands within the Arctic and Northern Temperate zones, and which is not to be accounted for by any theory of transport or variation, but which is agreeable to the hypothesis of all being members of a once more extensive flora, which has been broken up by geological and climatic causes.*' (see also quotes cited by Brundin, 1966).

Hooker was proposing vicariance as a mechanism for the differentiation of a widespread ancestral flora. This idea lapsed and was not revived until the next century (Herbert, 1935, 1950; Croizat, 1952, 1958), and only became generally accepted even later (Nelson & Rosen, 1981). Darwin did not accept Hooker's views on this, and in *Origin of Species* (Darwin, 1859), following the ideas espoused by Lyell (1837), invoked long distance dispersal as the mechanism for generation of similarities in Southern Hemisphere floras:

> '*...I am inclined to look in the southern, as in the northern hemisphere, to a former and warmer period, before the commencement of the Glacial period, when the antarctic lands, now covered with ice, supported a highly peculiar and isolated flora. I suspect that before this flora was exterminated by the Glacial epoch, a few forms were widely dispersed to various points of the southern hemisphere by occasional means of transport, and by the aid, as halting places, of existing and now sunken islands, and perhaps at the commencement of the Glacial period by icebergs. By these means, as I believe, the southern shores of America, Australia, New Zealand have become slightly tinted by the same peculiar forms of vegetable life.*'

Hooker (1860: xvi) was skeptical of Darwin's hypothesis:

> '*...the general distribution of species cannot be wholly accounted for by the supposition that natural causes have dispersed them over such existing obstacles as seas, deserts, and mountain chains...*'

However, Hooker was equivocal about the processes underlying the differentiation and dispersal of floras around the globe. There was no contemporary theory such as plate tectonics to support his embryonic notion of vicariance as an explanation for distant affinities between floras. He speculated about climatic change and movements of land-masses, both horizontally and vertically, as mechanisms driving migration, extinction and differentiation of floras.

Nevertheless, on his main point Hooker was consistent (Hooker, 1853, 1860, 1867: 25–26). Observing that trans-oceanic affinity among floras was a global phenomenon, he hypothesised that this pattern was an ancient one, and was the historical relic of a widespread, ancient flora that had evolved under different climates and configurations of land masses than prevail in the present. His primary interest, then, lay in understanding the evident pattern, and not in a fruitless search for unobservable past causes.

Hooker's (1860) major treatise on Australian biogeography in *Flora Tasmaniae* appears to have been misunderstood or misrepresented by some later authors. After careful analysis of the familial and generic makeup of the Australian flora, and comparison with that of other areas, he identified several 'elements' that he named according to their affinities: Indian, Australian, New Zealand and Polynesian, Antarctic, South African and European.

Later authors emphasised only three of these:

(1) an 'autochthonous' (= Hooker's 'Australian') group of mainly endemic taxa with distinct scleromorphic features and occupying temperate open communities,

(2) an 'Indo-Malayan' (= Hooker's 'Indian') element dominated by plants in tropical and subtropical rainforest and monsoonal habitats, and

(3) an 'Antarctic' element dominated by temperate rainforest taxa such as *Nothofagus*,

and attributed to Hooker the hypothesis that they migrated to Australia from elsewhere.

Barlow (1981) terms this the 'invasion theory', and provides an excellent review of its history. It was based on the assumption that the angiosperms did not evolve in Australia, but invaded the continent in three waves via various postulated 'land-bridges' (Van Steenis, 1962) from neighbouring regions that today support similar stocks of angiosperms. The first wave, via landbridges from the north, established the autochthonous group, which spread with little competition to occupy an empty continent and then diversified *in situ*. The second wave, from the south, contributed the Antarctic element, and later a third wave from the north contributed the Indo-Malayan element. The second and third waves, encountering already-adapted taxa, spread much more slowly and were only able to colonise those regions for which they were already pre-adapted. Hence, the Indo-Malayan flora remained confined to the tropical mesic and monsoon habitats of the north and east and the Antarctic element to the cool temperate and alpine regions of south-eastern Australia. For most of the next century, the invasion theory, with variations, formed the basis for discussions of Australian biogeography.

However, Hooker (1860) himself was very careful to avoid any suggestion of an invasion theory:

> '*In discussing the Antarctic vegetation of Australia, I shall have to adopt a style that appears to indicate that this flora is an immigrant, whereas it may, to a considerable extent, both in Australia and elsewhere, consist of altered forms of the plants of that continent, which have migrated from it to the Antarctic region.*' (p. xxxix)

and

> '*According to the hitherto prevailing theory of the distribution of plants, this presence of so many Indian species in tropical Australia would be accounted for by trans-oceanic migration, but this theory offers no explanation of the total absence of Australian species and typical genera in the tropical parts of India*' (p. l).

Throughout the essay, he states repeatedly that insofar as migration of flora may have occurred, he cannot identify the source or direction. In other words, he identified and named his elements only according to their affinities. He seems to have used the word 'migration' as a metaphor for affinity, not intending it to be taken literally.

Tate (1888) used Hooker's floristic elements in an analysis of the arid zone flora. Spencer (1896) used faunal groupings to divide Australia into three subregions, Torresian, Bassian and Eyrean, which have been accepted by most subsequent authors, with variations, for both flora and fauna. He recognised linkages of the Torresian subregion with northern Papuan biota, and linkages of the Bassian subregion with an Antarctic land.

Barlow (1981) discussed the views of others, such as Andrews (1916), Schwarz (1928) and Crocker & Wood (1947) who built on Hooker's ideas. Diels (1906), who concentrated his botanical forays in the south-west of Western Australia, hypothesised that this region was the centre of origin of the Australian (autochthonous) element of the flora. The high diversity of the south-western flora probably misled Diels as well as some other workers in their biogeographic interpretations. Hooker had speculated upon, but dismissed this possibility, again refusing to identify a centre of origin or direction of migration.

The invasion hypothesis reached its most detailed development in Burbidge’s (1960) floristic analysis of the vegetation of Australia. She concluded that there were distinct elements in the flora, recognising three main phytogeographic zones: Tropical, Temperate and Eremaean (Fig. 73). These equated well with Spencer's (1896) faunal regions (respectively Torresian, Bassian and Eyrean). Burbidge also identified three smaller 'focal areas' (exhibiting high endemism or diversity), in northern Queensland, south-western Australia and Tasmania, as well as the 'McPherson-Macleay overlap', whose high regional diversity was attributed to an overlap between the Tropical and Temperate zones. Although Burbidge espoused the idea that the present Australian flora was the result of evolutionary processes acting on immigrant floras, she also suggested that the autochthonous element might have been derived from some early Cretaceous element, echoing Hooker's original hypothesis. Karyological work by Smith-White (1954, 1959, and other papers, summarised in Barlow 1981) was seen to support this theory.

Perhaps Burbidge's most original contribution was to suggest that the arid-zone flora (especially those genera with warm-temperate links to the Northern Hemisphere) radiated from ancestors with cosmopolitan distributions on Cretaceous coastlines. These include endemic genera and species groups in the Aizoaceae *s. lat.*, Amaranthaceae, Asteraceae, Brassicaceae, Chenopodiaceae, and possibly others such as Convolvulaceae, Frankeniaceae and Portulacaceae. Burbidge considered that their habitat on coastal dunes and saline tidal flats pre-adapted them to the arid climate which set in during the Pleistocene (actually earlier, during the Pliocene). This suggestion has been adopted by subsequent authors such as Schodde (1989, see below).

Two major schools developed to explain the arrival of the different elements in the Australian flora, the so-called 'land-bridge theories' (Burbidge, 1960; Van Steenis, 1962 and references therein; Takhtajan, 1969) and the 'long-distance dispersal theories', originating with Darwin (1855, 1859) and furthered by, among others, Darlington (1965). Both of these schools had in common the twin ideas that the present exposed land areas were more or less fixed, apart from fluctuations of sea level, rise and erosion of island chains, and minor accretion and erosion of continental margins (although Darlington touched on the possibility of continental drift), and that the centre of origin of the Australian flora was outside the continent. They differed in the mechanisms proposed for migration of the flora, or its precursors, into Australia.

A third view was espoused by Herbert (1932, 1935, 1950, 1960, 1964, 1967). As Hooker (1860) had done before him, he believed that the Australian flora was derived from an ancient palaeotropical flora, which had existed on the continent since at least the early Mesozoic. He thought that the 'immigrant' elements hypothesised by other biogeographers such as Burbidge, were nothing more than the result of ecological and climatic sorting of an ancestral flora. He rejected migration via landbridges, pointing out they themselves would provide a sifting effect on communities.

Continental drift: a new paradigm

In 1915 Wegener presented his theory of continental drift, in which the continents were not fixed in place, but moved over time, splitting and uniting (Wegener, 1915). While geomorphologists were slow to accept Wegener's theory, mainly because a motive force for the continents was lacking, some biologists seized upon it as an explanation for observed biological distribution patterns. The idea that whole floras and faunas could be rafted about the surface of the globe on continent-size land masses, with all that that implied in terms of maintaining ecosystems more or less intact, of moving a range of habitats across climatic zones, and of moving organisms with little inherent vagility across vast distances over time, provided new possibilities for explaining biogeographic patterns. Several influential plant geographers, including Cain (1944) and Good (1947), clearly favoured continental drift as the major mechanism for movement of plants and floras, as opposed to long distance dispersal, although even as late as the mid-1960s there was no clear geophysical mechanism to explain the continental movement (Good, 1964). However, with geophysical research of the 1970s and 1980s revealing discoveries of mid-ocean ridges, sea-floor spreading and palaeomagnetism, geomorphology provided confirmation of Wegener's broad principles, and geomorphology and biogeography began to develop a strong feed-back loop, each supporting the other (Raven & Axelrod, 1974; Thorne, 1978; Coleman, 1980; Tarling, 1980; Beadle, 1981; Cocks, 1981; Whitmore, 1981; Axelrod & Raven, 1982; Raven, 1983; Briggs, 1987).

Here, then, was a paradigm shift (Cranston & Naumann, 1993). Under the old paradigm, the aim of biogeographic research was to identify the overseas centres of angiosperm origins and to trace the dispersal routes by which Australia received its stocks. This long-standing approach to biogeography attempts to explain the distribution of each taxon individually. It usually involves assuming a centre of origin from which some of the taxon's species either migrated or were displaced outwards. Criteria used to identify a centre of origin include a search for the most 'primitive' (hence oldest) living representatives, oldest fossils, and maximum diversity. An example here is the case of *Nothofagus* (Truswell *et al.*, 1987; Hill, 1994a, 1996). Conversely, Darlington (1957, 1965) considered that the more advanced members of a taxon occupy the centre of origin, because being competitively superior, they force the primitive, less competitive members outwards or to extinction. Other authors (Hennig, 1966; Nelson & Platnick, 1984; Brundin, 1988) proposed the 'progression rule', whereby speciation, and the evolution of novel features, occur only following dispersal out of the centre of origin. This would give the opposite pattern from that of Darlington. Authors proposing dispersal of a taxon consider modes of transport (whether active or passive), barriers against dispersal such as oceans, mountains or any unsuitable habitat, and ecological limitations on establishment in the new, distant habitat, which may be already occupied by functionally similar organisms (e.g. Darwin, 1855).

Reconstructing the history of an individual taxon in this way usually means proposing *ad hoc* hypotheses that cannot be corroborated, very often involving highly unlikely events with inestimable probability, such as a chance dispersal across an ocean. Such a hypothesis cannot be corroborated because unique past events cannot be observed directly, and because it makes no testable predictions.

The new paradigm involved evidence derived from palaeoclimatic and palaeontological studies and required a major change in thinking (Schodde, 1989):

> '*Whatever biotic elements Australia received before its break from Antarctica in the early Tertiary it inherited from Gondwana. If angiosperms did come into the region from the north in the Cretaceous, they came to Gondwana, perhaps even the Australian-sector of Gondwana; but not to Australia as such.*'

Thus with the acceptance of plate tectonic theory, it has been realised generally that it may not be productive to search for a point of origin of the angiosperm flora, and its migration paths. Although Raven & Axelrod (1974) still postulated an area of origin (in their case, 'Western Gondwana', which equates to Africa and South America), with subsequent migrations or transportations to their present distributions, this approach was rapidly becoming outdated. Instead, the evolution of the flora was interpreted as the gradual specialisation of a once more generally distributed biota (Barlow, 1981; Thorne, 1986; Webb *et al.*, 1986; Schodde, 1989). The existence of migration, or long-distance dispersal, is not necessarily discounted, but it no longer forms the generally accepted model for the origin of the majority of the Australian flora.

A diversification of approaches

From the late 1970s there has been an upsurge of interest in biogeographic studies of Australian biota, partly stimulated by the new theories of continental drift and cladistic biogeography, but also as a result of the establishment of the Australian Biological Resources Study, and consequent increase in taxonomic research.

Cladistic biogeography

Cladistic biogeography combines the power of cladistics to generate hypotheses about phylogeny and hence speciation with the notion that, if there is a congruent area pattern among many taxa, then one may postulate a single cause (Rosen, 1978; Nelson & Platnick, 1981; Page 1993b, 1994a, 1994b). Its development was heavily influenced by Croizat's notion of vicariance. Recognising that many related taxa were widely separated in different areas of endemism, Croizat (1952, 1958, 1962) had drawn lines on maps connecting such areas; these he called tracks. Where several tracks coincided he drew general tracks (Fig. 75), which he said represented vicariance events, that is historical splits between previously contiguous areas, causing isolation and speciation in their biotas. On a global scale, many general tracks cross oceans, and these have been interpreted as the legacy of splitting continents caused by plate tectonics (Rosen, 1978; Humphries & Parenti, 1986; Briggs, 1987). However, the primary purpose of general tracks is to indicate relationships between areas; they are not explanations in themselves.

Moreover, congruent patterns may have any common cause, such as concerted dispersal, and not necessarily vicariance. The exact cause does not matter as much as the question of whether there *is* congruent pattern. An hypothesis of congruence is testable and corroborable. If no general pattern emerges, then no general causes can be postulated.

Croizat's ideas strongly influenced the development of two disciplines: cladistic biogeography and panbiogeography (Croizat, 1958; Croizat *et al.*, 1974). Panbiogeography developed mainly in New Zealand, where its proponents attempted to develop quantitative methods for deriving general tracks from many partially coincident individual tracks (Craw & Weston, 1984; Page, 1987; Craw, 1989a, 1989b; Heads, 1989; Michaux, 1989; Grehan,

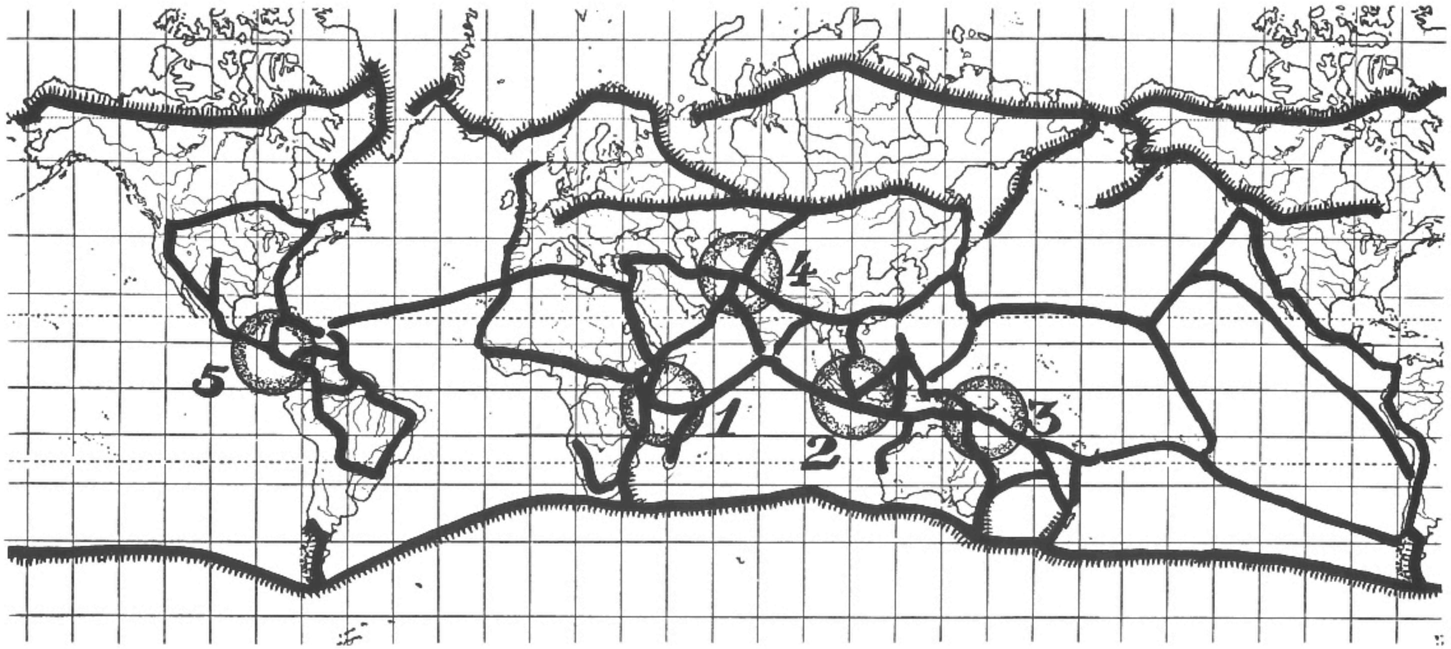

Figure 75. Leon Croizat’s (1958) main *general tracks* of the world. These trace lines of affinity in the distributions of plant and animal taxa on an intercontinental scale. Each general track represents congruence of many tracks of individual taxa. The hatched tracks are those considered *boreal* (Arctic) and *austral* (Antarctic). The numbered circles are *nodes*, or crossing points of multiple general tracks

1990; Michaux, 1994). This research program has been criticised (Seberg, 1986; Platnick & Nelson, 1988; Humphries & Seberg, 1989; Mayden, 1991) and largely abandoned in favour of cladistic biogeography, which explicity addresses history by using phylogenies.

Several cladistic methods have been used, reviewed by Morrone & Crisci (1995). A more recently developed method using paralogy-free subtrees (Nelson & Ladiges, 1996) extracts only the biogeographically relevant information from input cladograms, and at the same time eliminates most sources of error. It also has the considerable advantage of simplicity in concept and application.

There has been rapid growth in the use of DNA sequences to reconstruct phylogenies and these data are becoming a powerful tool in cladistic biogeography. While the sequence of branch-points in an area-cladogram shows the relative age of speciation events, independent information is needed to date these absolutely. The fossil record is one such source, and knowledge of this in Australia has progessed enormously in recent years (Hill 1994b; Hill *et al.*, this volume). However, given the gaps and uncertainties, such data will always be very approximate (Easteal *et al.*, 1995). The 'molecular clock' (rate of evolution as measured along the branches of a molecular phylogeny) has great potential as an alternative to fossils in dating ages of taxa (Parks & Wendel, 1990; Easteal, 1991; Harrison, 1991; Wendel & Albert, 1992; Thorpe *et al.*, 1994; Harvey *et al.*, 1995; Juan *et al.*, 1995). A confounding problem is that the molecular clock does not tick at a uniform rate – it varies both among taxa and between parts of the genome (Li & Tanimura, 1987; Penny *et al.*, 1987; Barinaga, 1992). Thus, to estimate age by a molecular clock it is necessary to understand the constraints of molecular and genome evolution, and there is a statistical problem: how to estimate the probability of being accurate (Albert *et al.*, 1994; Easteal *et al.*, 1995; Steel *et al.*, 1996). Biogeographic congruence in itself can be used to calibrate the molecular clock, because if many taxa are shown by cladistic biogeography to have speciated at the same time in response to the same causal event, then a molecular phylogeny of each taxon gives an independent estimate of the date of that event (Martin & Dowd, 1988; Page, 1990; Martin & Dowd, 1991). Moreover, the molecular clock has the potential to distinguish between vicariance, which causes simultaneous speciation in many taxa, and concerted dispersal, in which speciation events should not be contemporaneous (Page, 1990; Linder & Crisp, 1995).

Symposia

During the last 20 years, major symposia and multi-authored books have brought together the common threads in floral and faunal biogeography of Australia. These vary in geographic focus from regions within Australia to the whole Southern Hemisphere, e.g. the arid zone (Barker & Greenslade, 1981), Australia and New Guinea (Keast, 1981), the alpine region (Barlow 1986), the wet tropics (Kitching, 1988), the Southern Hemisphere (Ladiges & Humphries, 1991; Hill, 1993), the monsoon tropics (papers in *Aust. Syst. Bot.* 9(2), 1996) and the Pacific (Keast & Miller, 1996). A diversity of approaches is seen in these and other recent literature.

Descriptive and narrative studies

Concurrently with the development of an analytical approach to biogeography based on the theories of cladistic analysis and plate tectonics, descriptive and narrative studies on Australian biogeography have continued. Many have presented scenarios for taxa originating in one region and dispersing to others, e.g. angiosperms in general (Raven & Axelrod, 1974), the Australian flora in general (Beadle, 1981), plant taxa in the Malesian-Pacific region (van Steenis, 1963; van Steenis & van Balgooy, 1966; van Balgooy, 1975, 1984, 1993), Proteaceae (Johnson & Briggs, 1975), Proteaceae, Restionaceae and Myrtaceae (Johnson & Briggs, 1981), *Eucalyptus* (Pryor & Johnson, 1981), *Euphrasia* (Barker, 1986), *Acacia* (Maslin & Hopper, 1982). In general the palaeobotanical community has continued to use this approach (Truswell *et al.*, 1987; Hill, 1994b; Pole, 1994), although the role of vicariance too is sometimes acknowledged (Hill *et al.*, this volume).

As part of a work dividing the world into 35 floristic regions, Takhtajan (1986) treated continental Australia as three regions: Northeast, Southwest, and the Central, or Eremaean Region. These regions were further divided into provinces. A new and much more useful classification of Australasian biotic regions was published by Schodde (1989), integrating flora and fauna into five mapped elements (Fig. 74) and accounting for their origins by a combination of plate tectonics, climate change, radiation and extinction. This scheme is discussed in detail below.

Studies on individual taxa

Many researchers have investigated the phytogeography of individual groups, as a spin-off from taxonomic revisions. Initially these tended to be descriptive treatments with narrative analyses of the historical causes of the observed distribution patterns (e.g. most papers in Barker & Greenslade, 1981). Increasingly, such studies have been based on phylogenetic reconstructions, although they have mostly focussed only on the history of the individual group: where it originated and the taxon-specific sequence of events (vicariance, dispersal and extinction).

Australian studies on individual taxa include eucalypts (Myrtaceae) in eastern, southern and south-western Australia (Ladiges *et al.*, 1983; Ladiges *et al.*, 1984; Ladiges & Humphries, 1986; Ladiges *et al.*, 1987; Humphries *et al.*, 1988; Thiele & Ladiges, 1988; Ladiges *et al.*, 1989; Ladiges *et al.*, 1992; Wardell-Johnson *et al.*, 1997); Sapindaceae along a track from eastern Australia to Malesia and the Pacific (Turner, 1995, 1996); *Euphrasia* in temperate Australia (Barker, 1986); *Boronia* sect. *Valvatae* (Rutaceae) throughout non-arid Australia (Duretto, 1995); Embothrieae (Proteaceae) in eastern Australia, New Guinea and South America (Weston & Crisp, 1994); *Lechenaultia* sect. *Latouria* (Goodeniaceae) (Morrison, 1987) and *Leptosema* (Fabaceae) (Crisp, 1982) in the south-west, centre, north and north-east of Australia; *Gossypium* (Malvaceae) in northern and central Australia (Wendel & Albert, 1992); *Oreobolus* (Cyperaceae) in Australia and the Pacific (Seberg, 1988); and *Guioa* (Sapindaceae) in Malesia and Australia (Van Welzen, 1989).

A recent approach seeks to identify ancestral areas for individual taxa, assuming that there has been a history of range-expansion or dispersal rather than vicariance (Bremer, 1992, 1995; Ronquist, 1994, 1995). The 'cost' of dispersal is traded off against extinction. Ronquist (1997) has refined the method to take vicariance into account, at no extra cost. Unlike the narrative dispersalist biogeography of Darlington *et al.* (above), this method offers the possibility of corroboration by recurrent single patterns where concerted dispersal has occurred, or by geological hypotheses. Hypothesised migrations of sets of floristic elements, e.g. across Torres Strait or the Tasman Sea, could be explored by these methods. This sort of analysis should be especially applicable where a history of island-hopping with speciation is suspected, such as along the Hawaiian chain (Wagner & Funk, 1995) and the Melanesian arcs (Turner, 1995; Polhemus, 1996). Swenson & Bremer (1997) applied this approach to *Abrotanella* (Asteraceae), which occurs in Australia and across the Pacific.

Are general explanations possible in biogeography?

Although cladistic biogeography is based on the expectation of congruent geographic patterns among different taxa, this assumption may be false. It appears that in some areas of endemism, such as South America, co-existent elements of the biota have different area-patterns suggesting different biogeographic histories (Parenti, 1981; Humphries & Parenti, 1986; Crisci *et al.*, 1991a, 1991b; Nelson & Ladiges, 1996: 52–53). Such areas are sometimes termed 'composite'. Composite patterns probably arise via diverse causes: sequential accretion of land fragments carrying different organisms to form present-day land masses and biota; taxa responding differentially to vicariance events; patterns of different age overlain in the same areas; and patterns reflecting different causes, e.g. migration versus vicariance. It seems reasonable to suppose that any ancient area would be affected by such complexities.

In the face of such complexity, is it possible to find general patterns with common cause, or should every taxon be considered to have its own unique history, incongruent with any other? Some would believe that the search for congruent patterns is delusive:

> 'Nothofagus *probably had a similar centre of origin to many other southern taxa, but its history of dispersal is unique. There have almost certainly been some episodes of long distance dispersal involved, which would not have been followed exactly by other taxa, and even its land based dispersal is unique. The overall message is that biogeography is not amenable to sweeping generalisations, and when they are applied it is more an expression of ignorance than of profound understanding.*' (Hill, 1996).

If this conclusion is true, then biogeography cannot progress beyond the narrative stage. However, there is good theoretical and empirical evidence that congruent area patterns exist (Edmunds, 1981; Cracraft, 1986, 1991; Crisci *et al.*, 1991a; Seberg, 1991; Page, 1993b, 1994a; Linder & Crisp, 1995; Nelson & Ladiges, 1996). Moreover, general patterns and general explanations will never be found if they are not sought. Therefore, the only option is to continue to seek general area-patterns, and also to subject the results to rigorous test. Page (1988, 1989) has proposed statistical tests of congruence among area-cladograms and has implemented them in his programs. Further studies are needed in this area, especially in developing null hypotheses for statistical tests. More work is needed also in developing methods that can discover multiple, overlain general patterns, if such exist, and statistical tests as to whether these are different. Where overlain patterns are of different age, the molecular clock may be used to distinguish them (Page, 1993b). Methods already exist that can hypothesise dispersal as an *ad hoc* event against a background of cospeciation (vicariance), but for greater explanatory power a method is needed that combines both processes in a single optimised procedure (Page, 1994a, 1994b).

Analytical studies in search of general pattern

Some studies, unfortunately relatively few, have looked for general patterns through combined analysis of multiple taxa. Phenetic studies have usually had an ecological emphasis and aimed to define 'phytochoria' (floristic regions), often within particular taxonomic groups, e.g. rainforests (Webb & Tracey, 1981; Webb *et al.*, 1986; Whiffin & Hyland, 1986), freshwater aquatics (Jacobs & Wilson, 1996), grasses (Simon & Macfarlane, 1996), Triticeae (Poaceae) throughout Australia (West *et al.*, 1988) and *Acacia* (Hnatiuk & Maslin, 1988).

Invoking processes: palaeobotany, geology, ecophysiology and climate

Once floristic patterns have been identifed and described, biogeographers attempt to explain them by recourse to various earth processes. During the 1980s and 1990s studies have continued in the quest to understand the past geological and climatic complexity in the Australian region and how these have impacted upon the flora and fauna. These studies are summarised in the present volume by Frakes and Hill *et al.*, where it is shown that the history of the Australian flora and fauna is far more complex than previously suspected. As well as the gross sorting of the biota resulting from the fragmentation of Gondwana, major climatic changes have apparently driven migrations of floras backwards and forwards over the continent. These migrations have been accompanied by periods of major extinction. Expansion of floras back into areas decimated by aridity, glaciation and other factors have also undoubtedly led to major episodes of rapid speciation. For example, Schodde (1989) hypothesised that the central arid zone has acted as a sink, which was filled by speciation out of the near-coastal regions during wetter periods, then emptied by extinction in the subsequent arid periods. Present biogeographic patterns, then, represent just one iteration of biotic sorting, and past distributions were often quite different.

Some papers in this re-evaluation through climatic and palaeobotanical studies are particularly worth mentioning. Truswell *et al.* (1987) addressed the biogeographic consequences resulting from reassessment of geophysical activities that have taken place on the northern margin of the Australian plate. The accumulated fossil data indicate that the Indo-Malayan element of the Australian flora, as postulated by Burbidge particularly, might not be entirely Laurasian, but that there has been some floristic interchange between Australia and regions to the north in the late Cretaceous and early Tertiary. However, Truswell *et al*. (1987) found little fossil pollen evidence for any 'massive influx of taxa' into Australia from the north following the Miocene contact about 15 Ma.

This view was supported by Webb *et al*. (1986), who doubted that Australian rainforests arrived by dispersal from external sources and put forward a different interpretation, based on floristic comparisons between rainforest provinces. They suggested that Australia's rainforests, rather than being depauperate samples of those of south-east Asia, are 'remnants of the ancient Gondwanan flora that once covered Australia'.

In an analysis of the origins of the flora of Australia's wet tropics, Barlow & Hyland (1988) concluded that the tropical rainforests of northern Australia are the complex products of a sequence of palaeogeographic and palaeoclimatic events. They invoked a combination of refugial surges and contractions, and intermixing of autochthonous New Guinea and Australian rainforest flora elements with those of Malesia. This scenario recapitulated that of Van Steenis (1979), who suggested that the Malesian and Australian floras are re-mixing after a long separation, as exemplified by palms now found in Australia and New Guinea.

Hooker's elements today

We have reviewed the history of thinking about the origins and relationships of the various 'elements' that comprise the present-day Australian flora. In a sense this has come full circle. Hooker's primary concern was to identify broad-scale patterns by teasing out the different 'elements' in the Australian flora. Each element denoted a different floristic affinity between Australia and other regions of the world; thus his elements are essentially similar to the 'tracks' which we discuss below. Note that Hooker's elements, like tracks, are not mutually exclusive areas on a map - they intermix and overlay in space and time. He speculated about the processes that might cause strong affinities to cross oceans, suggesting that they are relics of ancient and widespread floras that were broken up by climatic and geological upheavals. However, he was careful not to commit himself to any explanation, such as migration in a particular direction: that was in the past and therefore unobservable.

For most of the 20th century, biogeographers accepted Hooker's main elements and debated their origins, whether by the 'invasion theory' (Burbidge, 1960; Barlow, 1981; Beadle, 1981), by *in situ* differentiation (Herbert, 1935, 1950, 1960, 1964, 1967) or by plate tectonics (Barlow, 1981; Schodde, 1989). Many present-day biogeographers, like Hooker, prefer to eschew causal explanations of distributional patterns until these patterns have been elucidated, analysed and tested for generality (Rosen, 1978; Nelson & Platnick, 1981; Ladiges, 1998). This is the approach we use in the following sections.

Diversity and endemism of the Australian flora

The earliest botanists to visit Australia were struck by the unique character of its plants. As pointed out by Hooker (1860) and Barlow (1981) this curious characteristic is partly the result of the ubiquity of a few genera (*Eucalyptus* and *Acacia* in particular) and partly of high diversity and endemism in some distinctive groups (Proteaceae, Myrtaceae, Casuarinaceae, Epacridaceae and some of the conifers). However, on analysis this peculiarity is mainly limited to lower taxonomic levels, e.g. species and genus. (Data for this analysis are drawn from various sources: Morley & Toelken, 1983; Harden, 1990; Groombridge, 1992; Boden & Given, 1995; Mabberley, 1997 and the *Flora of Australia*, including figures for unpublished volumes). At higher taxonomic levels the uniqueness diminishes, with few families being confined solely or largely to the continent. The composition of the Australian flora above family level is virtually identical with that of other areas. For example, the proportions of species in major groups of vascular plants in Australia are very similar to those for the world as a whole (Table 17).

Table 17. Numbers and proportions of species in major groups of vascular plants in Australia

		Vascular plants	Pteridophytes	Gymnosperms	Monocots	Dicots
Australia	No.	18 640	470	75	3723	14 372
	%	*100*	*2.5*	*0.4*	*20.0*	*77.1*
World	No.	260 140	9800	840	55 800	193 700
	%	*100*	*3.8*	*0.3*	*21.4*	*74.5*

Comparison of the ten largest families in Australia (cf. Introduction, Table 3) with those in the world as a whole (Table 18) again shows our flora to be a fairly representative sample. Seven families are common to both lists. The three large Australian families that are not in the world top ten (Proteaceae, Epacridaceae and Goodeniaceae) are among those that give the Australian flora its distinctive aspect. It is interesting to note that 140 years ago, Hooker (1860), working with a sample of only 8000 known species, gave a nearly identical list of the largest Australian families.

Table 18. The ten largest families of Australian vascular plants, in descending order of size, compared to those in the world as a whole.

Australia		World	
Fabaceae *s. lat.*[1]	2400	Asteraceae	22 750
Myrtaceae	1858	Orchidaceae	18 500
Poaceae	1302	Fabaceae *s. lat.*[1]	18 000
Asteraceae	1221	Rubiaceae	10 200
Proteaceae	1116	Poaceae	9500
Orchidaceae	650	Euphorbiaceae	8100
Cyperaceae	650	Lamiaceae	6700
Epacridaceae	424	Scrophulariaceae	5100
Euphorbiaceae	395	Myrtaceae	4620
Goodeniaceae	377	Cyperaceae	4350

[1] The legumes are here treated as a single family, *contra* Cronquist but the consensus view of legume systematists.

Australia is recognised as a major centre of floristic endemism. The concept of an area of endemism is fundamental to historical biogeography. Authors have long observed that small geographic regions often contain many endemics – species that occur nowhere else. These endemics are often unrelated or, when they are closely related, they have differing ecological requirements. Moreover, geographically distant areas of endemism often contain species that are closely related and have similar ecological tolerances (Candolle, 1820; Wallace, 1855; Croizat, 1958, 1962; Nelson, 1978; Nelson & Platnick, 1981). An excellent example is the *Nothofagus* forests and alpine floras of the distant southern continents that so struck Hooker (1860). Surprisingly, narrow endemism is often maintained despite the apparent vagility of the organisms. For example, Wallace (1855) noted that birds did not cross the 25 km strait between Java and Sumatra. These authors inferred that if widely separated areas contain related taxa then perhaps the areas were united in the past but subsequently separated, causing the taxa within them to speciate (Croizat, 1958, 1962; Nelson & Platnick, 1981; Page, 1993b). Thus, areas of endemism are units of evolutionary history, rather than of ecology.

Islands are the most easily defined areas of endemism; they have an obvious boundary — the sea (Wagner & Funk, 1995). However, islands often occur in groups, and there may have been a history of successive differentiation events among them, as in the Malesian region. This history may be represented as a tree, with the branch-points representing divergence of areas (vicariance events), analogously with a phylogeny of organisms (Nelson & Platnick, 1981: 398–409). Islands vary continuously in size, up to the scale of continents, and virtually all are (or contain) areas of endemism (Major, 1988; Andersson, 1994). At the scale of continents, the break-up of Gondwana into the present-day southern continents during the last 160 million years is well known as a series of events reflected in the phylogeny of their endemic biota (Rosen, 1978; Humphries & Parenti, 1986; Weston & Crisp, 1994; Linder & Crisp, 1995). Further, within each continent and larger islands there are areas of endemism such as mountain ranges, lakes and other more subtly delimited regions. These may have a history of differentiation also. Thus areas of endemism may be expected to form a hierarchy, reflecting history at different geographic scales and different time scales.

Given this hierarchy of scales, how are areas of endemism to be defined for biogeographic analysis? Some authors (Platnick, 1991) suggest that we should use the smallest recognisable units, analagous with species at the base of the hierarchy of organisms. Henderson (1991) states that we should not use areas at all, for fear of circularity when we later draw inferences about areas from the results of biogeographic analysis of taxa. This is analogous to rejecting the circumscription of taxa before phylogenetic reconstruction for fear of prejudicing conclusions about taxa (Vrana & Wheeler, 1992). However, there is no need to restrict areas of endemism to the smallest diagnosable unit. Just as one can reconstruct a phylogeny using accepted higher taxa as the terminal units, so it should be possible to reconstruct a history of areas using more inclusive units, such as the southern continents. In both cases, one would be reconstructing a deeper history than if one were using less inclusive taxa as terminal units.

Takhtajan (1986) treats the continent of Australia as a high-level area of endemism. It is one of only six floral kingdoms in the world, and the second smallest in extent, after the Cape Kingdom of southern Africa. Of the 280 vascular plant families in Australia, Takhtajan considered 18 endemic. His list has been outdated by considerable change in family delimitations, resulting from molecular phylogenetic studies. However, in the most recent family-level classifications (Bremer *et al*., 1998; Chase *et al*., in press), 16 angiosperm familes are recognised that are endemic to Australia. In systematic sequence, these are Austrobaileyaceae, Atherospermataceae, Blandfordiaceae, Boryaceae, Doryanthaceae, Xanthorrhoeaceae, Dasypogonaceae, Anarthriaceae, Ecdeiocoleaceae, Tetracarpaeaceae, Cephalotaceae, Tremandraceae, Akaniaceae, Emblingiaceae, Gyrostemonaceae and Eremosynaceae). To these should be added the fern family Platyzomataceae. This total of 17 families is high compared with the other small floral kingdoms: the Cape Kingdom has eight endemic or near-endemic familes, and the Holantarctic Kingdom has 12 (Takhtajan, 1986). Other families, such as Eupomatiaceae, Casuarinaceae, Centrolepidaceae, Hydatellaceae, Epacridaceae, Stackhousiaceae, Myoporaceae, Goodeniaceae and Stylidiaceae are near-endemic, having few species outside the continent. Also very characteristic of the Australian flora are the Chenopodiaceae, Proteaceae, Cunoniaceae and Pittosporaceae. At species level, Australia has one of the highest levels of endemism in the world (c. 80%, Groombridge, 1992; c. 95%, Boden & Given, 1995) compared with other large countries, e.g. South Africa (70–80%), Madagascar (68–80%), New Caledonia (c. 80%), Indonesia (67%), China (40–56%).

As might be expected, endemism at the generic level is intermediate between family- and species-level endemism. About 566 of the 2500 genera recognised in Australia are endemic, and the largest families (not surprisingly) contain the largest numbers of genera. Endemism at generic level is spread very unevenly across families, and the largest genera (Introduction, this volume, Table 19) have most of their species richness outside the tropics.

Within Australia endemism is spread unevenly, and several centres of endemism have been recognised. According to Takhtajan (1986), there are over 150 endemic genera in his North-east region (being the north and east coasts and adjacent inland), 125 endemic genera in the South-west and 85 endemic genera in the Eremaean region. On an areal basis, this represents a heavy concentration of endemics in the south-west. Similarly, at species level, endemism is greatest in the south-west, with 68% of species endemic and 83% near-endemic (Boden &

Given, 1995). Burbidge (1960) recognised four floristic areas of 'special interest and importance', being centres of high diversity and endemism: the South-west Province, Tasmania, North-east Queensland and the McPherson-Macleay overlap. Cracraft (1991) recognised 14 areas of endemism for the purpose of a cladistic biogeographic analysis of Australia, based on bird distributions and Burbidge (1960). Crisp *et al.* (1995) adopted Cracraft's scheme with modification (Fig. 76).

The 'centres of plant diversity and endemism' recognised by Boden & Given (1995) for mainland Australia include four that are more or less the same as Burbidge's (South-west Botanical province, Western Tasmanian Wilderness, Wet Tropics of Queensland and the Border Ranges), plus five others (Table 19). In a comparison among these areas (Table 19), again the south-west is exceptional in both species richness and endemism, although it should be noted that its area is an order of magnitude greater than most of the others. When area is taken into account, the Wet Tropics of north-east Queensland is perhaps an even more outstanding centre of diversity and endemism. The species richness and endemism are not much less than in the south-west, but in an area only one thirtieth the size (Table 19). Moreover, this region has 43 endemic genera and is noted for its concentration of the world's primitive angiosperm families (13 out of 19; Boden & Given, 1995).

Table 19. Centres of plant diversity and endemism recognised in mainland Australia by Boden & Given (1995), showing their estimated number of vascular plant species and the percentage of these that are endemic.

	Area (km^2)	No of species	% endemic
Australian Alps	30 000	780	11
Border Ranges	6000	1200	7
Central Australian Mountains	168 000	1300	9
Kakadu-Alligator Rivers	30 000	1430	3
North Kimberley	99 000	1476	7
South-west	310 000	5500	68
Sydney Sandstone	24 000	2200	2
Western Tasmania	14 000	800	?
Wet Tropics	11 000	>3400	43

In many ways, the South-west and Wet Tropics present a complete contrast as centres of endemism. The South-west has a mediterranean climate and sclerophyllous vegetation of heath, mallee and eucalypt forests and woodlands, while the Wet Tropics has a tropical wet climate and rainforest vegetation. As Hooker (1860) first noted, the large and characteristically Australian families (e.g. Goodeniaceae, Epacridaceae, Stylidiaceae, Casuarinaceae, Proteaceae, Myrtaceae, Myoporaceae etc) have most of their diversity in the south-west, or in the south-east, but never in the tropics. This same pattern is shown by the largest two genera, *Acacia* (Hnatiuk & Maslin, 1988) and *Eucalyptus s. lat.* Wardell-Johnson *et al.*, 1997). By contrast, the Wet Tropics has more genera and families, many of which are scarcely seen outside the rainforest pockets of the east coast, and which therefore are not considered 'characteristically Australian' (Webb *et al.*, 1986).

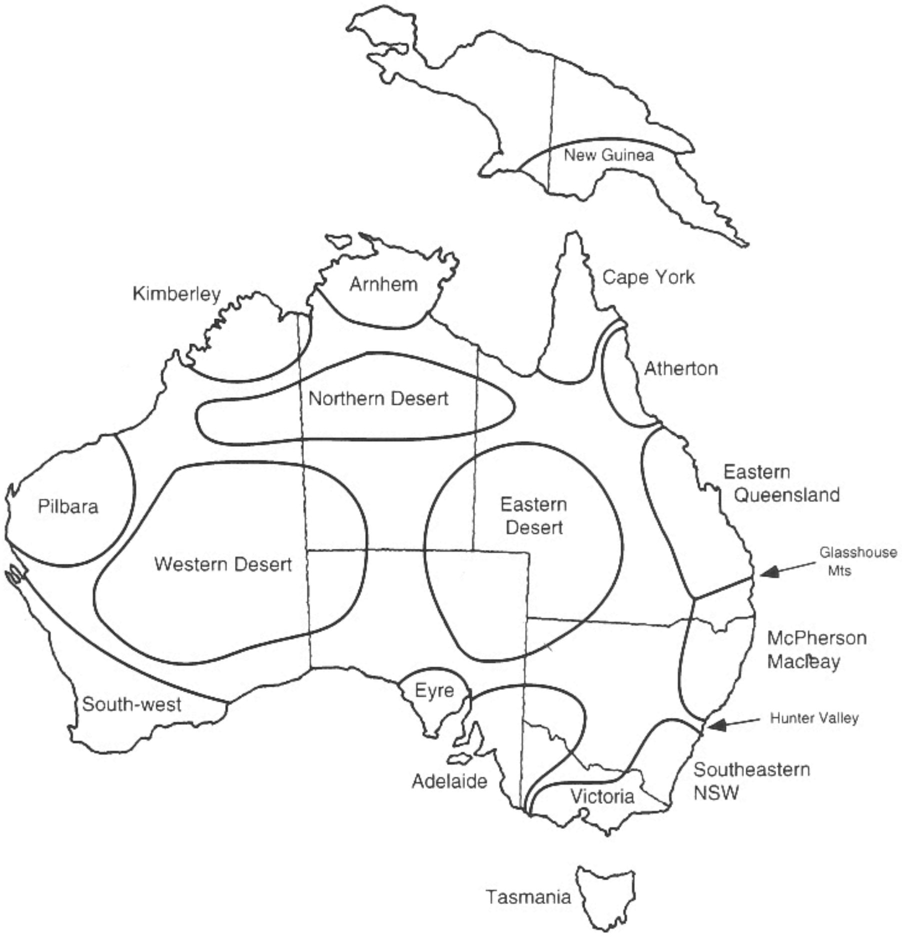

Figure 76. Map of Australia and New Guinea, showing major areas of endemism as in Crisp *et al.* (1995: fig. 3). Modified from Cracraft (1991) by adding 'New Guinea', splitting his 'Southeastern forest' into 'Southeastern New South Wales' and 'Victoria', and by splitting his 'Eastern Queensland' into 'McPherson-Macleay' and a smaller 'Eastern Queensland'. Note that there are gaps between the mapped areas, by contrast with maps of biotic regions (Figs 73 & 74). These gaps occur because areas of endemism represent coinicident sets of range-restricted species, and ignore widespread species (and minor areas of endemism) that occur in the gaps.

Relationship of Australian flora to other floras

Track analyses

In this analysis, first we compile general tracks, then we relate these to phylogenies where available, and finally we make process interpretations. We do not attempt to overlay the vast number of distribution maps available, but rather synthesise from the literature the generalised tracks that have been used. Where there is a dearth of these, we develop the general maps without rigorous analysis, using coincident widely distributed taxa. Widespread taxa are difficult to interpret. Often they are regarded as the results of dispersal, and thus uninformative (Morat, 1986; Nelson & Ladiges 1991, 1996). However, it could be argued that a recurrent widespread pattern is a track, and possibly informative on plant history.

We summarise the distributional data into four general tracks: the South Pacific track; the Equatorial track; the Trans-Indian Ocean track and the Pan-temperate track.

South Pacific track

The South Pacific track consists of two sections. The first is the disjunction across the southern Pacific, illustrated by the very numerous taxa shared between Australia, New Zealand and southern South America. This is possibly one of the best documented and studied disjunctions. It was first noted by Hooker (1853), and subsequently there have been many enumerations of the taxa that span it (Croizat, 1958; Thorne, 1972, 1978, 1986; Good, 1974; Takhtajan, 1986; Crisci *et al.*, 1991b). Some 50 genera and seven families are restricted to southern South America and Australasia. In addition, there are several closely related generic groups, e.g. *Drimys/Tasmannia/Pseudowintera* and *Austrotaxus/Pilgerodendron/Libocedrus/Papuacedrus*. The conifer flora is almost entirely restricted to this track (Page & Clifford, 1981).

The South Pacific track has long been recognised, and was called the Antarctic element by Hooker (1860) and Burbidge (1960), a term widely used in the 'pre-drift' literature. Subsequent to the acceptance of continental drift the track has generally been called 'Gondwanan' (e.g. Turner, 1995 and many other references). Since Gondwana contained many more components than this track, this is a misleading usage. It would be tempting to call it the *Nothofagus* track, as this well-studied genus spans the whole track, but it may also be misleading to call a general track after a particular taxon.

The fossil evidence for a common flora from southern South America (Axelrod *et al.*, 1991), Antarctica (Dettmann, 1989; Askin, 1990; Truswell, 1990), Tasmania (Hill & Read, 1987; Hill, 1992), New Zealand (Pole, 1993) and southern Australia (Truswell, 1993; Hill *et al.*, this volume) from the Late Cretaceous to the early Tertiary is extensive. The flora, often described as the Gondwanan flora (or the *Nothofagidites* floristic province), contains many of the floristic elements still associated with the *Nothofagus*-dominated forests of the same areas, as well as several taxa now found in the montane uplands of New Guinea. Prominent taxa included *Nothofagus*, *Araucaria*, Proteaceae (*Beauprea*, *Banksia*), Winteraceae, *Ilex*, Podocarpaceae, and many others. The vegetation has been described as cool temperate, with no temperature extremes – a climate currently associated with the cool uplands of tropical areas (Specht *et al.*, 1992). The fauna associated with these forests has been shown to be sharply discontinuous with that of the surrounding vegetation types (McQuillan, 1993), thus corroborating the uniqueness of this biota.

The second, northern part of the track has been less studied, and shows complex patterns around the northern and eastern borders of Australia, encompassing New Guinea, West Malesia, New Caledonia and eastwards to Fiji. There is very little fossil evidence from these northern areas (Veblen *et al.*, 1996), so reconstruction of this track can only be based on extant distributions (Turner, 1995; Weston & Crisp, 1996).

Table 20. Selected distribution patterns of members of the South Pacific track.

Taxon	New Guinea	New Caledonia	Monsoon Australia	Temperate Australia	Tasmania	New Zealand	Temperate South America
Nothofagus	+	+	+[1]	+	+	+	+
Drimys/ Tasmannia/ Pseudowintera	+	+	+	+	+	+	+
Cupaniopsis[1]	+	+	+				
Jagera	+		+				
Carpha	+			+	+	+	+

Source: [1] fossil evidence only (Veblen *et al*., 1996)

The presence of a wide range of taxa associated with the *Nothofagidites* flora, including *Nothofagus,* in New Guinea firmly establishes the island as part of the South Pacific track. Similarly, many of these taxa also occur on New Caledonia, which also shares the largest two components of its flora with Australia and New Guinea (Morat *et al.*, 1986). This establishes the north-eastern part of Australia, New Guinea and New Caledonia as part of this general track, and enables us to include in this track taxa more or less restricted to these areas (Table 20). We therefore argue that patterns which apply to part of the track, can be taken to apply to all taxa of that particular track. This acceptance of at least a portion of the monsoonal forests as part of the 'Gondwana' biota is well established in the Australian literature (Barlow, 1981; Webb *et al.*, 1986; Turner, 1995).

Equatorial track

This track encompasses the equatorial regions of the world: Amazonia in South America, equatorial Africa (as scattered forests), Madagascar, India and south-east Asia (Croizat, 1968). This track has been called the tropical element in Australia (Burbidge, 1960), although her concept may have included taxa present only in the monsoonal parts of New Guinea and north-eastern Australia, taxa which we would ascribe to the South Pacific track. Schodde's (1989) Irian element clearly belongs to this track.

Specht (1981) showed that some 177 genera (10% of the Australian genera) show Afro-Indo-Malesian distribution patterns. These genera are most common in the tropical and subtropical closed forests. This assessment is corroborated by Hartley (1986), who documented the distribution ranges of 716 genera of New Guinean rainforest species. Based on these data it is evident that there is substantial evidence of the equatorial track reaching Australia (Table 21). The most common pattern includes Africa and Indo-Malesia (57.7%, 413 of the 716 genera), while a further 20% (140 of 716 genera) are amphi-equatorial. Only 20% of the genera are more or less restricted to New Guinea, New Caledonia and Australasia.

The equatorial track is largely coincident with the Late Cretaceous *Palmae* palaeo-floristic province, which included most or all of Africa and Madagascar, eastern South America, India and probably south-east Asia (Herngreen & Chlonova, 1981; Crane, 1987). Interestingly, all of Australia is usually mapped to the *Nothofagidites* province, but it is not clear how good the fossil evidence is for the northern margins of the continent. Thus the possibility that the northern parts of Australia may have been part of the *Palmae* palaeofloristic province cannot be discounted on the plant evidence.

Table 21. Selected genera showing the equatorial track. All genera are present in Australia.

Taxon	New Guinea	SE Asia	India	Madagascar	Africa	South America
Celtis	+	+	+	+	+	+
Beilschmiedia	+	+	+	+	+	+
Ilex	+	+	+	+	+	+
Eugenia s. str.	+	+	+	?	+	+
Flagellaria	+	+	+	+	+	
Antiaris	+	+		+	+	
Garcinia					+	
Myristica	+	+				
Freycinetia	+	+				
Cansjera	+	+				
Macadamiinae	+				+	+

Trans-Indian Ocean track

This track is not well documented (but see Croizat, 1968), and consists mainly of temperate elements (e.g. Proteaceae subfam. Proteoideae, Restionaceae, Haemodoraceae, *Wurmbea*, *Ehrharta*/*Microlaena*, *Schismus/Plinthanthesis, Anacampseros*). These are taxa which cross the Indian Ocean, but which do not occur in Malesia, India or Sri Lanka. This absence distinguishes this track from the Equatorial track (above). Those taxa which occur in South America are more or less restricted to eastern South America (e.g. Haemodoraceae; Simpson, 1990). Earlier phytogeographical studies over-emphasised this track (see comments in Burbidge, 1960), possibly because of the ecological prominence of the Restionaceae and Proteaceae in the south-western tip of South Africa and south-western Australia.

There are also some rather bizarre disjunctions across this interval. *Bulbinella* is shared between Africa and New Zealand; *Cunonia capensis*, which is widespread in temperate African forests, is the only non-New Caledonian member of its genus; and *Dietes robinsoniana*, found on Lord Howe Island, is the only non-African member of its genus (Goldblatt, 1981). However, these examples should be regarded as anecdotal within the larger biogeographical sweep. Unique events cannot be explained.

Table 22. Examples of Indian Ocean tracks.

Taxon	Africa	Madagascar	Indian Ocean islands	Australia	New Zealand
Adansonia	+	+		+	
Proteeae	+	+		+	+
Ehrharteae	+	+	+	+	+
Wurmbea	+			+	
Anacampseros	+			+	

Pan-Temperate track

This track includes all temperate areas, in both the southern and Northern Hemispheres. At higher latitudes it reaches sea-level, while at lower latitudes its members are found at higher altitudes. In Australia members of this track generally co-occur, often in the same habitat, with members of the South Pacific track. However, members of the South Pacific track are absent from the Northern Hemisphere, and from Africa. It might be argued that the South Pacific track is a subset of the Pan-temperate track, as it occurs over a subset of the areas occupied by the Pan-temperate track. However, in the South Pacific track the closest relatives of the track members in Australia are in New Zealand or South America, while it appears likely that the closest relatives of the Pan-temperate track members in Australia are in the Northern Hemisphere. If the two tracks were combined, this information might be lost, so we deem it better to keep them separate in this analysis.

Members of this track, typically, are *Festuca*, *Poa*, *Euphrasia* (Table 23) while taxa such as *Gaultheria*, *Rhododendron* and *Vaccinium* show a more limited distribution area.

This track is generally continuous along the temperate zones of Asia, Europe and North America, but its southern extensions are largely interrupted, forming small outliers on mountain tops. Burbidge (1960: 179) refers briefly to this group of taxa, including in addition to those tabulated below, *Mentha*, *Ajuga*, *Stellaria*, *Viola*, *Centaurium*, *Drosera*, *Ranunculus* and *Hydrocotyle*. Many taxa in this track are extensive in the Northern Hemisphere but reach their southern limit in New Guinea, e.g. *Castanopsis*, *Potentilla* and *Gentiana s. str.*

Table 23. Examples of Pan-temperate patterns. Sources: [1]West & Garnock-Jones (1986); [2]Barker (1986).

Taxon	West Malesia	Himalayas	Europe	North America	South America	Africa
Poa	+	+	+	+	+	+
Festuca	+	+	+	+	+	+
Rhododendron	+	+	+			
Scleranthus[1]			+			
Euphrasia[2]	+	+	+	+	+	

Differentiation within the tracks

General tracks link the individual distribution patterns of taxa (species, genera, families) into a general statement, which can be interpreted in terms of the areas occupied by those tracks (Fig. 75). If the general track is at supra-specific level, then it includes areas with different species. This differentiation in the biota along the track can be investigated using cladistic biogeography, and the patterns retrieved are indicative of the relationships among the floras from different parts of the track, and of the factors that may have led to that differentiation. Relatively few cladistic biogeographical studies have been published, thus hampering this interpretation.

South Pacific track

The Antarctic track comprises two parts. The first is the southern portion, which differentiated over Australia, New Zealand and South America. The second is the northern portion, which differentiated over the northern and eastern parts of the Australian craton, involving New Guinea, Queensland, Northern Territories, New Caledonia and further east to Fiji.

The southern portion of the Antarctic track has stimulated much research. This is largely because it poses a relatively simple question: is the biota of New Zealand more closely related to that of South America, than to the biota of Australia. In the last decade, a second question has been added: is the biota of New Zealand derived (by long-distance dispersal) from that of Australia, or are they both derived from a common ancestral biota?

The most popular tool used to address these questions has been one of the versions of cladistic biogeography. The earliest studies were by Humphries (1981, 1983), and like the later studies, these were centered on *Nothofagus*, the genus of southern beeches. These studies seek congruence in the area relationships of as big a suite of taxa as are available. Seberg (1991) used five taxa, but failed to find congruence among them, and Crisci *et al.* (1991b) similarly failed to find congruence. This lack of congruence was largely due to a faulty phylogeny of *Nothofagus*.

The most recent study on this problem (Linder & Crisp, 1995) was based on a total evidence phylogeny of *Nothofagus*, which was based on both morphological data (from Hill & Jordan, 1993) and sequence data from the chloroplast encoded *rbc*L gene (Martin & Dowd, 1993). In addition, all other taxa which are informative on these areas, and for which phylogenetic hypotheses are available, were used. Included were *Aristotelia*, *Cyttaria*, Restionaceae, Iridaceae, Haemodoraceae, Danthonieae, Cunoniaceae, Embothrieae, *Oreobolus* and Winteraceae. Component analysis was used to find the tree which best fitted the area relationships, while minimizing the number of duplications required (Page, 1993a, 1993b).

Linder & Crisp interpreted their results as suggesting that the flora of Australia and New Zealand differentiated from a common flora, shared more recently than with temperate South America. This is contrary to the results obtained for three insect groups – chironomid midges (Brundin, 1966), mayflies (Edmunds, 1981; Cranston & Naumann, 1991) and the dipterans *Symmerus* plus *Austrosymmerus* (Munroe, 1974) – which suggest that the Australian biota has a more recent connection to South America than to New Zealand. Also, Ladiges *et al.* (1997) extracted a non-paralogous subtree from *Aristotelia* in Linder & Crisp's data, showing support for the third possible relationship between these three areas: (Australia, ((New Zealand, South America)). It appears unlikely that more than one of these three interpretations can be correct, unless New Zealand is a composite area. There is substantial evidence that in fact New Zealand is a composite area, possibly with one portion linking to Antarctica and South America, and the other to Australia (Craw, 1989a; Walley & Ross, 1991; Kroenke, 1996).

Recently, Pole (1994) suggested that the New Zealand flora is entirely derived by long-distance dispersal from Australia, that is, it is a derivative biota, a specialised form of the Australian flora. The implications are that the New Zealand flora and vegetation formations would be uninformative about the Gondwanan Tertiary *Nothofagus* forests, as they are derived from the Australian, and not the Gondwanan, *Nothofagus* forests.

It is evident that the relationships between the floras of Australia and New Zealand are complex. For some taxa, commonality appears to be based on trans-Tasman dispersal. Garnock-Jones (1993) showed that a dispersalist explanation for the occurrence of *Hebe* in Australia and New Zealand is more parsimonious than a vicariance explanation. This was also postulated for *Scleranthus* species shared between New Zealand and Australia (West & Garnock-Jones, 1986). Similarly, Swenson & Bremer (1997) explained the occurrence of two related species of *Abrotanella* in Australia-New Guinea and New Zealand by dispersal from the latter. However, for many other taxa (Linder & Crisp, 1995, and in prep.) this is not the case. It is possible that concerted dispersal down the westerlies might produce a similar pattern to vicariance; this can be tested by establishing the ages of the disjunction using molecular clocks. Vicariance would predict a similar age for all taxa, while concerted dispersal might predict different ages.

Martin & Dowd (1993) suggested that it might be possible to date the divergence among the subgenera of *Nothofagus*, using the *rbc*L DNA sequence. They used the first fossil occurrence of *Nothofagus* pollen at 83 Ma as a reference point, and this suggested a divergence date of 66 Ma for subgen. *Lophozonia* and 48 Ma for subgen. *Fuscuspora*, the two subgenera disjunct between South America, New Zealand and Australia. These dates are substantially less than the estimated date of geological isolation between New Zealand and

Australia, and indicate either long-distance dispersal, or errors either in their calculations or in the geological reconstructions.

Another differentiation in the South Pacific track is around the northern margins of the Australian craton, and the fragments separated from the craton during the Late Cretaceous and Tertiary. Much of this flora is found in the monsoonal forests of this region (Webb *et al.*, 1986). A number of pertinent questions arise from this area:

(1) What was the sequence of isolating events in this area? Was the Kimberley region isolated before central New Guinea?

(2) Could the extension of the track to New Caledonia (and by implication to the other islands of the Inner Melanesian Arc) and Fiji be ascribed to dispersal or vicariance?

(3) Is the frequent extension of Gondwanan species to Western Malesia (Java, Sumatra, Borneo, Sulawesi) reflecting ancient distribution patterns, or dispersal?

The most informative work on the biogeography of this area has been by Van Welzen *et al.* (1992) and Turner (1995), working mostly on the Sapindaceae. Turner's analyses of eight genera (*Mischarytera*, *Arytera*, *Rhysotoechia*, *Cnesnocarpon*, *Guioa*, *Cupaniopsis*, *Lepidopetalum* and *Jagera*) presents the most detailed review of the current understanding of the biogeography of the area. Turner delimited 25 areas of endemism, ranging from the western end of New Guinea to Samoa in the east and Lord Howe Island to the south (Fig. 77).

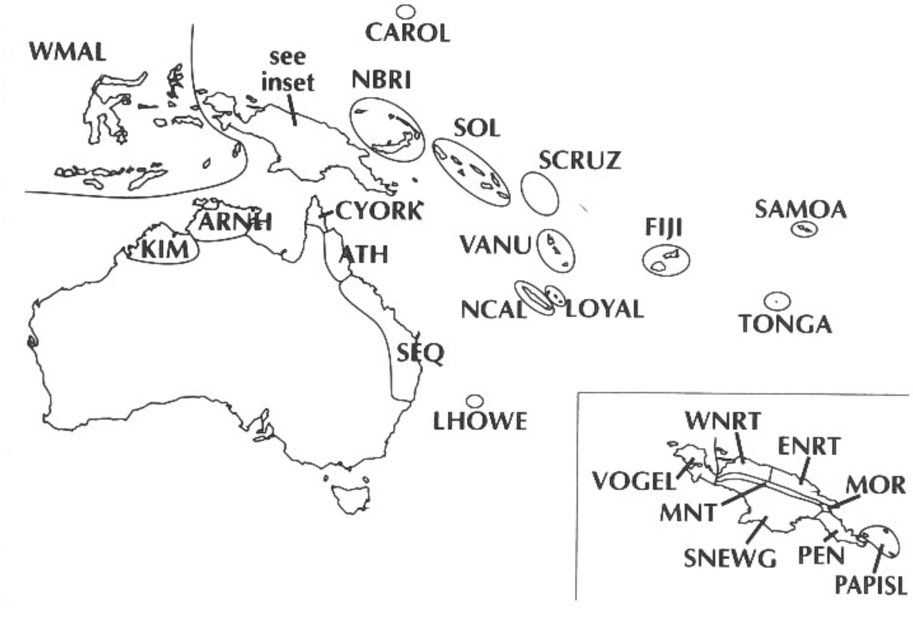

Figure 77. The 25 areas of endemism employed by Turner (1995) in his biogeographical analysis of eight genera of Sapindaceae. Abbreviations: SEQ, south-east Queensland and northern New South Wales; ATH, Atherton Tableland; CYORK, Cape York; ARNH, Arnhem Land; KIM, Kimberley Plateau; SNEWG, south New Guinea; PEN, peninsula; MOR, Morobe; ENRT, east north New Guinea; WNRT, west north New Guinea; MNT, central mountain range; VOGEL, Vogelkop; WMAL, west Malesia; NBRI, New Britain; PAPISL, Papuan Islands; SOL, Solomon Islands; SCRUZ, Santa Cruz archipelago; VANU, Vanuatu archipelago; LOYAL, Loyalty Islands; NCAL, New Caledonia; LHOWE, Lord Howe Island; FIJI, Fiji Islands; SAMOA, Samoa; TONGA, Tonga; CAROL, Carolina Islands. Reproduced with permission.

Turner obtained the following results:

(1) The eastern Australian areas consistently form a monophyletic group with south-eastern New Guinea.

(2) Eastern Australia + south-eastern New Guinea are sister to the rest of New Guinea.

(3) These areas are sister to the Outer (Fiji, Samoa) and Inner (New Caledonia, Loyalty Islands, Lord Howe Island) Melanesian Arcs. These arcs are either monophyletic or paraphyletic at the base of the area cladogram.

In order to return to explanations of individual taxa, Turner optimised the cladograms for each of the taxa onto the selected area cladogram, and assessed the number of dispersal and extinction events required for each node on the area cladogram. This allows subjective assessment of the likelihood of vicariance or dispersal explaining the patterns.

Turner interpreted these results as suggesting two vicariance events; the first separating the Inner Melanesian Arc (IMA) from the Australian craton, the second separating New Guinea (not including south-eastern New Guinea) and Australia (Fig. 78). The presence of the sapindaceous genera to the west of New Guinea, and on the Outer Melanesian Arc (OMA), he ascribed to dispersal. Similarly, he suggested that the West Malesian extensions are the result of dispersal. Non-congruence among area-cladograms for different taxa is taken as evidence for dispersal: for example the sister-position of West Malesia differs among the different area cladograms, indicating different sources for the migration.

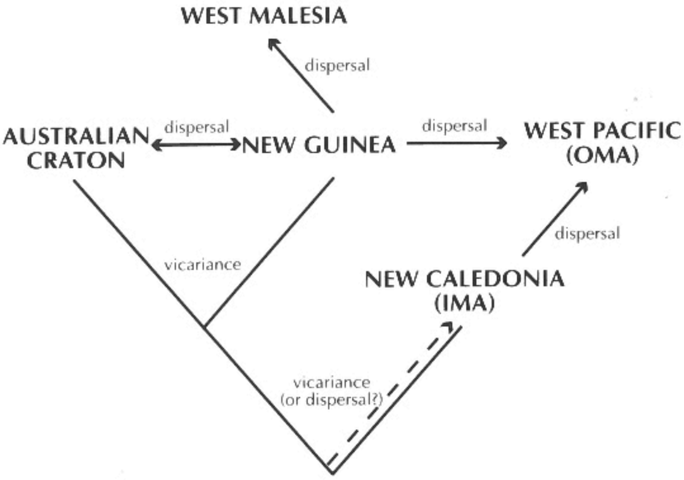

Figure 78. Summary of the major events affecting the Sapindaceae in the Gondwanan biota, from Turner (1995). Areas in this diagram are groupings of those in Fig. 77 as follows: Australian Craton (KIM, ARNH, CYORK, ATH, SEQ); West Malesia (WMAL); New Guinea (VOGEL, WNRT, MNT, ENRT, MOR, SNEWG, PEN, PAPISL); New Caledonia/IMA (NCAL, LOYAL, LHOWE); West Pacific/OMA (CAROL, NBRI, SOL, SCRUZ, VANU, FIJI, SAMOA, TONGA). Reproduced with permission.

Both New Zealand and New Caledonia form part of the Inner Melanesian Arc. Yet their floras are rather different (Morat *et al.*, 1986). If both floras shared a terrane separated from Australia, they should have rather similar floras. This lack of similarity has not yet been adequately investigated.

The northern border of the track is assumed to coincide with the complex boundary between Asian- and Australian-derived terranes and microcontinents (Michaux, 1994).

Equatorial track

This track is poorly understood, and there appear to be no cladistic biogeographic analyses of any members of the track. However, there are several hypotheses on the relationships between the Australian members of the track and those from other areas. Hooker (1860) recognised the track but was non-committal about any direction of migration. Several authors have suggested that the Australian members of the track invaded from Malesia (the 'invasion theory' discussed above, see Barlow, 1981). Herbert (1967 and earlier cited references) argued that they differentiated *in situ* from an ancient, pan-tropical flora. Specht (1981) suggested that these taxa are a remnant of a Gondwanan flora. Truswell *et al*. (1987) indicated that there is no fossil evidence of the monsoonal rainforest taxa being relative newcomers in Australia: the fossil record precedes the collision between the Australian and Sunda Shelf plates. They support various suggestions that the tropical flora is ancient, part of a pan-equatorial flora that may have flanked the Tethys in the Late Cretaceous.

The continental reconstructions of Audley-Charles (1987) do not provide for a continuous landmass linking south-east Asia and Australia, but Audley-Charles suggests that there has been a continuous traffic of continental fragments from Australia across the Tethys to south-east Asia. These may have been sufficiently close together to have acquired the developing equatorial flora. However, Veevers (1984, 1991) presents a different view, of the Sunda and Melanesian arcs having been more or less continuously in contact in the mid-Tertiary. Australia pushed through this line after about 20 Ma, broke it and distorted Sundaland. This scenario does not include a regular traffic of north-moving terranes and may provide a better model for integrating the northern portions of Australia into the Equatorial track.

Cladistic biogeographical studies of this biota are required to establish whether the elements of the equatorial track in northern Australia are part of a differentiating ancient *Palmae* flora, or whether they are derivative elements that established recently due to long-distance dispersal from West Malesia.

Trans Indian Ocean track

There have been few studies of this track. Linder & Crisp (1995) included several taxa from this track in their global analysis, and these do not indicate any close relationships. However, a number of rather striking, and common, taxa are shared between Africa and Australia.

The recognition of this track in cladistic biogeography is dependent on a pattern of (Australia, (Africa, South America)) rather than the typical *Nothofagidites* pattern of (Africa, (Australia, South America)). There are several plant taxa that show this areal relationship, including Haemodoraceae (Linder & Crisp, 1995) and *Anacampseros* (Gerbaulet, 1992). In addition, recognition of the track is based on a composite South America, where the eastern, tropical portion is assumed to have a different history from the southern, temperate portion. This division was suggested by Humphries (1981), Parenti (1981) and Crisci *et al*. (1991b).

The track can be accounted for by vicariance, but the dates for the opening of the Indian Ocean (c. 120 Ma: Veevers, 1984; Scotese *et al.*, 1988) are rather early for angiosperm differentiation. The pattern is consistent with an earlier disjunction across the Indian, rather than across the central Atlantic Ocean. But such a scenario would predict that the absence of these taxa from India is secondary. Another possibility is dispersal eastward across the Indian Ocean. Support for this hypothesis is found in the scattered occurrence of African taxa on the Indian Ocean islands: *Ehrharta sp.* (Gibbs Russell & Ellis, 1987) and *Disa borbonica* (Linder, 1981) on Reunion and *Pentaschistis insularis* (Linder & Ellis, 1990) on Amsterdam Island. In these cases, the species on the islands is not a basal member of the clade, but has close relatives on the African mainland. It is possible that some of the patterns may be due to vicariance (Restionaceae, Proteaceae), but others may be due to dispersal (*Wurmbea*, *Ehrharta*). Baum *et al.* (1998) postulated on the basis of a molecular clock that the disjunction in *Adansonia* between Africa, Madagascar and Australia is due to long-distance dispersal across the Indian Ocean. They argue that the relatively short branches separating the species within *Adansonia*, compared to the branchlengths separating *Adansonia* from related genera, also indicate a recent diversification within the genus. There is a need for further studies on unrelated groups to establish the generality of this pattern.

The occurrence of Restionaceae and Casuarinaceae on Ninetyeast Ridge (Kemp & Harris, 1975) dated to the Paleocene or Late Oligocene could indicate either relictual fragments of a wider Indian flora, or secondary dispersal from Australia.

This still leaves the nature of the relationship between the floras of Africa and Australia open. Clearly there is a direct link, but how it was established is not yet clear.

Pan-Temperate track

The occurrence of Eurasian temperate taxa in Australia has generally been interpreted as the result of long-distance dispersal from Eurasia down the Malesian mountains to Australia (Burbidge, 1960; Raven, 1973). There are relatively few cladistic analyses of these widespread taxa: most of the taxa are large (e.g. *Festuca*, *Poa*, *Euphrasia*), and hence present great difficulties to the phylogenetic systematist. However, the analyses of West & Garnock-Jones (1986) of *Scleranthus* and Barker (1986) of *Euphrasia* present some evidence that if migration occurred along the track, it may have been from Australia north to Eurasia.

There is as yet no continental drift model postulating continuous land between Australia and Eurasia, along which vicariance could have developed. Hence a long-distance dispersal model appears the most feasible, but the dispersal could have been in either, or both, directions.

Relationships among the four tracks

Tracks can be arranged in a hierarchical fashion, from the narrowest track to a single global explanation (cf. Amorim & Tozoni, 1994). It could, for example, be argued that the track linking temperate Australian rainforests with those of New Zealand and South America is a distinct track from that linking the monsoonal forests of New Guinea, Queensland and New Caledonia. However, the analysis of taxa spanning these two tracks indicates that there are two nodes of differentiation along the same track, and that they are united at a higher level of generality. Similarly, there should be a similar relationship among the four general tracks discussed above. Only a global analysis can resolve this relationship. Current indications are that the equatorial and the South Pacific tracks are the major vicariant patterns, and that these probably differentiated shortly after the origin of the angiosperms. The relative timing and position of the Trans-Indian Ocean track is not known. The Pan-temperate track may also have developed rather later, and if the indications that its presence in the southern Hemisphere is due to dispersal, then it cannot be related to the other two tracks.

Of interest here could be the biogeographical patterns of some of the widespread Proteaceae subtribes, like Macadamiinae and Hicksbeachiinae (Weston & Crisp, 1996). It is possible that the Proteaceae contain elements in the equatorial, trans-Indian and South Pacific tracks: consequently an understanding of their relationships could be informative.

Synthesis

The flora of Australia is most closely related to that of its Gondwanan neighbours: in the south, New Zealand and southern South America; to the north New Caledonia and New Guinea. These relationships appear to be most parsimoniously explained as sister-group relationships, rather than derivative, ancestor-descendent relationships. This implies that all these areas have autochthonous floras relative to each other, all are informative on the ancestral biota that once covered the whole area.

This implies that there are derivative floras within Australia. The most striking must be the savanna floras associated with the eucalypt woodlands on richer soils, and the sclerophyllous heaths, mallees and eucalypt forests of the oligotrophic soils.

However, this picture is partially upset by elements that do not fit: the trans-Indian Ocean links to Africa, and south-east Asian links. It is not clear whether there were any other island or continental links across which their biota could have vicariated, or whether these links are the result of long-distance dispersal across the Indian or Tethys Oceans. The relationship to the equatorial track is also enigmatic, and requires the analysis of members of this track, to determine the extent of its presence on mainland Australia, and whether these taxa are here as a result of dispersal, or whether they were originally part of a pan-equatorial flora.

Phytogeography within Australia-New Guinea

Here we present a descriptive classification of the biotic regions of Australia and New Guinea and a narrative account of their origins. Then we review recent analyses of distributional patterns using cladistic methods. This section covers only the most recent studies on the Australian flora.

Biotic regions

The most recent attempt to synthesise Australia's flora in a few broad biotic regions is that of Schodde (1989). Giving credit to a long line of predecessors, from Hooker (1860) to Burbidge (1960), Schodde states that his scheme contains only 'minor but significant modifications to the traditional concepts of Australian biotic elements'. This claim is too modest, for he is the first author to use both animal and plant distributions as evidence, and he adds two rainforest elements that have not been recognised explicitly before - at least, not since Hooker.

Note the subtle distinction between two kinds of biotic units: 'elements' (defined by hypothesised origin) and 'regions' or 'zones' (defined geographically). Hooker (1860) and Herbert (1967) described elements, whereas Spencer (1896) and Burbidge (1960) mapped regions or zones. Schodde integrated both kinds in a single system of mapped 'elements' (Fig. 74), each of which is defined by content (floristics and faunistics) as well as hypothesised history.

Schodde mapped most of mainland Australia and Tasmania with three elements: Torresian, Bassian and Eyrean (Fig. 74). These correspond closely with Spencer's faunistic regions of the same names and Burbidge's Tropical, Temperate and Eremaean floristic zones. The Torresian element comprises tropical eucalypt savannah woodland and semi-deciduous forest with a monsoonal climate. This element also occurs in southern New Guinea and has strong links with south-east Asia and beyond, for instance the Eurasian sylvid warblers have radiated here. The Bassian element is temperate eucalypt woodland and forest with a sclerophyll shrub understorey, dominated by autochthonous genera of the Myrtaceae, Fabaceae (especially *Acacia*), Proteaceae and Epacridaceae. The climate is mostly cool to warm temperate with winter rainfall, grading to a summer maximum in the north-east. There is strong differentiation between and endemism within the disjunct south-eastern and south-western regions. The Eyrean element is the arid-adapted biota of central Australia, vegetated by desert steppes (Chenopodiaceae), hummock grassland (*Triodia*), and tall shrubland to low woodland of mulga (*Acacia*) and mallee (*Eucalyptus*). Reptiles are diverse here but otherwise this element is the poorest in vertebrates. However, there is a very rich fossil vertebrate fauna from central Australia (Vickers-Rich *et al.*, 1991). Taken together, these three elements largely correspond with Hooker's Australian element ('autochthonous' element of later authors). However, the monsoonal component of Hooker's Indian element falls into Schodde's Torresian element.

Schodde recognised two additional elements, Tumbuna and Irian, both being rainforest types (Fig. 74). These reach their maximum extent in New Guinea, which was not included in previous biotic classifications of Australia. It has now become clear that at least southern

New Guinea has always been part of the Australian craton. The Tumbunan element is cool temperate to subtropical rainforest dominated by trees of *Nothofagus*, Podocarpaceae, Lauraceae, Myrtaceae, Proteaceae, Cunoniaceae, Elaeocarpaceae and Winteraceae. The vertebrate fauna includes the primitive myobatrachid and leiopelmatid frogs, side-necked land turtles, ratite birds, parrots, other non-passerines, the ancestral specialised songbirds, monotremes and the major lineages of marsupials The Irian element is tropical rainforest with strong Malesian affinity, which dominates the lowlands of New Guinea but in Australia occurs only in small pockets on Cape York Peninsula, Arnhem Land and the Kimberley. To a considerable extent, these two elements revive Hooker's scheme. Tumbuna corresponds closely with his Antarctic element, and Irian is his Indian element minus the monsoonal component.

In hypothesizing origins, Schodde took full advantage of the plate tectonics paradigm, which was not available to his predecessors. This led directly to his recognition of the Tumbunan element, which is now widely considered to be a scarcely modified, *in situ* relic of the Eocene forests of Gondwana (cf. Hill *et al.*, this volume), hence the derivation of the name Tumbuna, from a Melanesian pidgin word meaning ancestor. Not surprisingly, this element is also found in those fragments of Gondwana that still have cool to warm, humid temperate climates: New Zealand, southern and tropic-montane Africa ('Afromontane forest') and southern South America. Schodde considered the Tumbunan element ancestral to the autochthonous biota of the Torresian, Bassian and Eryean elements. As the climate dried out and became more seasonal from the late Miocene onwards, and fire became a major influence, the characteristically Australian sclerophyll flora radiated. With onset of aridity in the Pliocene, the Eyrean element appeared in the centre of the continent. This is the most depauperate of the elements: Schodde viewed the arid zone as a sink, 'fed by the plumbing and taps' of the surrounding scleromorphic flora, only to be emptied by extinction during the arid cycles of the Plio-Pleistocene. Thus Schodde largely abandoned the old invasion theory of mass immigration. The only exception is the Irian element and the monsoonal forest component of the Torresian element, which were seen as a southerly extension of Malesian (and even pantropical) biotas.

Tracks within Australia

Here we turn our attention to evidence of floristic tracks within Australia. Tracks are not the same as a biotic region, which is a coherent mapped area circumscribed by a characteristic floristic content, climate and geography.

Identifying tracks within continents is problematic. Clearly there has been geographical differentiation within the Australian flora, as recognised by previous authors from Hooker to Schodde. For the purpose of analysis, it is necessary to partition this variation into geographic units - areas of endemism (as distinct from biotic regions). Continents and islands define themselves as areas by their coastline. By contrast, the continuous land mass of a continent seldom has sharp internal boundaries, except lakes and high mountain ranges, which are often likened to islands. Where there are no sharp boundaries, one cannot expect sharply differentiated areas of endemism (or tracks).

A further problem is that through geological history a succession of taxa is likely to have differentiated within the same (or parts of the same) areas at different periods. This is more likely to have happened within continuous land masses, where there are fewer barriers to the dispersion of flora. This too leads to an expectation that different subsets of the present flora are likely to show different tracks for the same areas.

Continent-wide tracks

The only published cladistic analyses of areas across the whole of Australia using multiple taxa have concerned vertebrates, mainly birds (Cracraft, 1982, 1986, 1991) and several angiosperm families (Crisp *et al.*, 1995). All these studies used more or less the same set of areas, which are derived partly from Fig. 73 (Burbidge, 1960) and partly from the distributional limits of species of plants (Crisp *et al.*, 1995) and vertebrates (Cracraft, 1991).

Figure 76 shows the version used by Crisp *et al*. (1995). Cracraft's most general hypothesis (Cracraft, 1991) was based on a broad sample of vertebrates (mammals, snakes, lizards, frogs and birds). He used parsimony analysis of endemicity, and has been criticised for using only widespread distributions, which lack historical information content (Nelson & Ladiges, 1991, 1996; Crisp & Weston, 1995; Crisp *et al*., 1995; Stafford Smith *et al*., 1995). Cracraft's area-cladogram for all vertebrates (Fig. 79a) shows a basal divergence between a track linking the South-west to Adelaide, and the rest of the continent. Tasmania is unresolved at the base. The remaining areas split into a desert track and another connecting the east coast and tropics. The wet tropics (Atherton) are closely related to the adjacent monsoonal areas (Cape York, Arnhem Land and the Kimberley). On this basis, Cracraft hypothesises an ancient vicariance event running east-west along the Nullarbor Plain, followed by another event separating eastern and northern areas from the arid inland.

Crisp *et al*. (1995) used phylogenies of eleven taxa from the angiosperm families Fabaceae, Goodeniaceae, Malvaceae, Myrtaceae and Proteaceae to investigate the biogeography of Australasia. Unlike Cracraft they included New Guinea in their study, but deleted some areas for which data were insufficient (Pilbara, Eyre and Eastern Desert). General area-cladograms were built using Page's tree-mapping method, implemented in Component 2.0 (Page, 1993a). The preferred general area cladogram from Crisp *et al.* is shown in Fig. 79b. It differs from Cracraft's (Fig. 79a) mainly in having an early split between a tropical track (Kimberley, Arnhem, Cape York, New Guinea and Northern Desert) and the rest (except Tasmania, which is basal). Also, the South-west is most closely related to the Western Desert rather than to the south coastal areas, and the wet tropics are related to eastern and southern coastal areas, rather than to the monsoonal areas.

However, Crisp *et al.* found that by repeating the analyses using different subsamples of the taxa, different results were obtained (Crisp *et al.*, 1995: fig. 3). This was due to conflict between the area-cladograms derived from individual taxa (Crisp *et al.*, 1995: fig. 4). Moreover, the tree-mapping method appears to introduce artefacts when constructing general area-cladograms (Ladiges *et al.*, 1997). Reanalysis of these data using the paralogy-free subtree method (Nelson & Ladiges, 1996) confirms that there is no single general area-cladogram derivable from the data of Crisp *et al.* (Ladiges, 1998).

If there is no unique history relating all angiosperm taxa within Australasia, then perhaps cliques (subsets) of taxa are identifiable that share a common track. Using the method of Nelson & Ladiges (1996), we have extracted the paralogy-free subtrees from the data of Crisp *et al.*, and sorted these by hand into sets that do not conflict and are combinable into resolved general area-cladograms (Fig. 80). To the original data we have added *Cullen* (Fabaceae) (Grimes, 1997) and removed stringybark eucalypts and *Banksia*, which contain no relevant paralogy-free information. We have simplified the areas by amalgamation (old areas from Fig. 76 in parentheses): New Guinea (New Guinea), Tasmania (Tasmania), Wet tropics (Atherton), Monsoon tropics (Kimberley, Arnhem, Cape York), South-east (Eyre, Adelaide, Victoria, South-eastern NSW, McPherson-Macleay, Eastern Queensland), South-west (South-west), Central Australia (Pilbara, Western desert, Eastern desert, Northern desert).

The largest fully resolved clique includes five subtrees from four taxa: *Daviesia latifolia* group (2 subtrees), *Leptosema* (1 subtree of 2), *Persoonia* and *Cullen* (Fig. 80a). This tree has Tasmania at the base, then the South-east, Monsoon tropics, South-west and Central Australia in phyletic sequence. A second clique (Fig. 80b) includes the same subtrees except that *Lechenaultia* is substituted for *Persoonia*, and differs only in the relationship of the terminal three areas. This difference reflects a conflict between the individual subtrees from *Persoonia* and *Lechenaultia*. *Persoonia* relates the South-west more closely to Central Australia than to the Monsoon tropics, whereas *Lechenaultia* relates the South-west more closely to the Monsoon tropics. However, both cliques agree on a track in which there is initial isolation of Tasmania then the South-east from the tropical, central and western areas. A third clique (Fig. 80c), comprising *Gossypium* and a second subtree from *Leptosema*, specifies a track differentiating first the Monsoon tropics, then Central Australia, then the

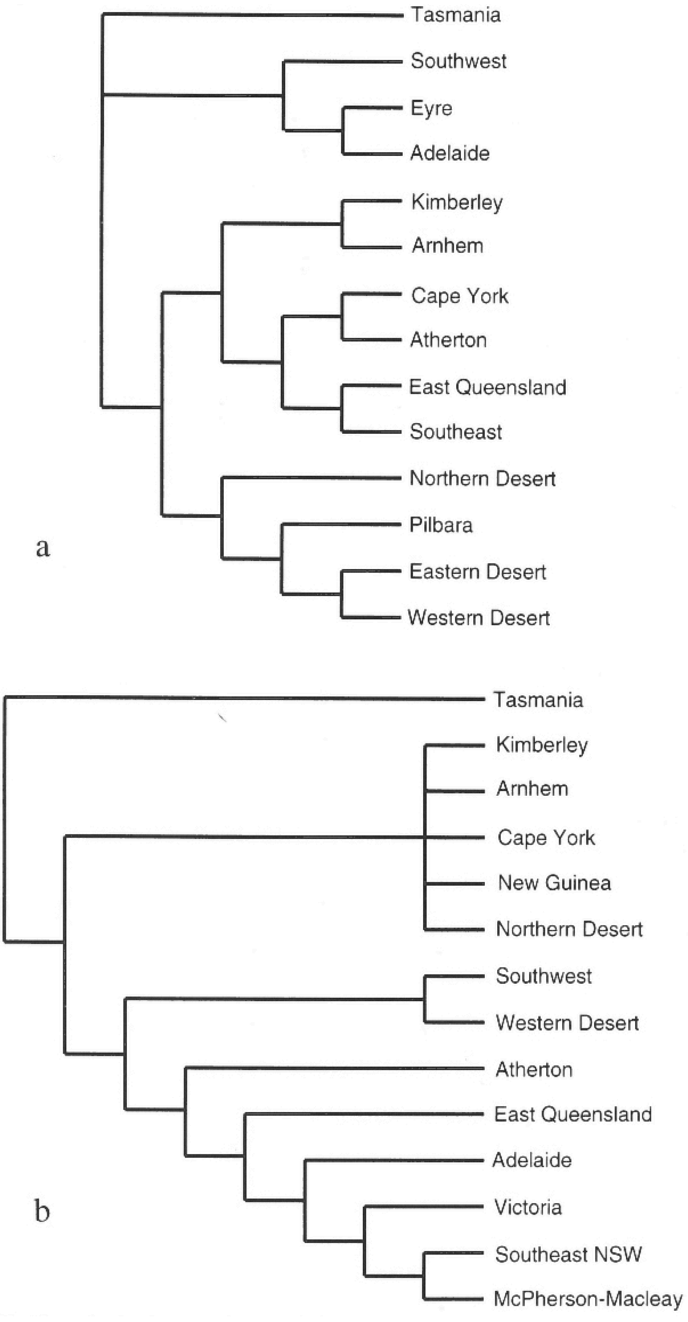

Figure 79. Hypothesised general area-cladograms for Australia and New Guinea derived from congruent pattern in plants and animal distributions. Areas are as in fig. 43 (Cracraft, 1991). **(a)**, derived from distributions of birds, mammals, snakes, lizards and frogs. Some areas differ from those in Fig. 76 — see caption. **(b)**, derived from phylogenies of 11 taxa in Proteaceae, Myrtaceae and Fabaceae (Crisp *et al.*, 1995). Areas Eyre, Pilbara and Eastern Desert are deleted due to lack of data.

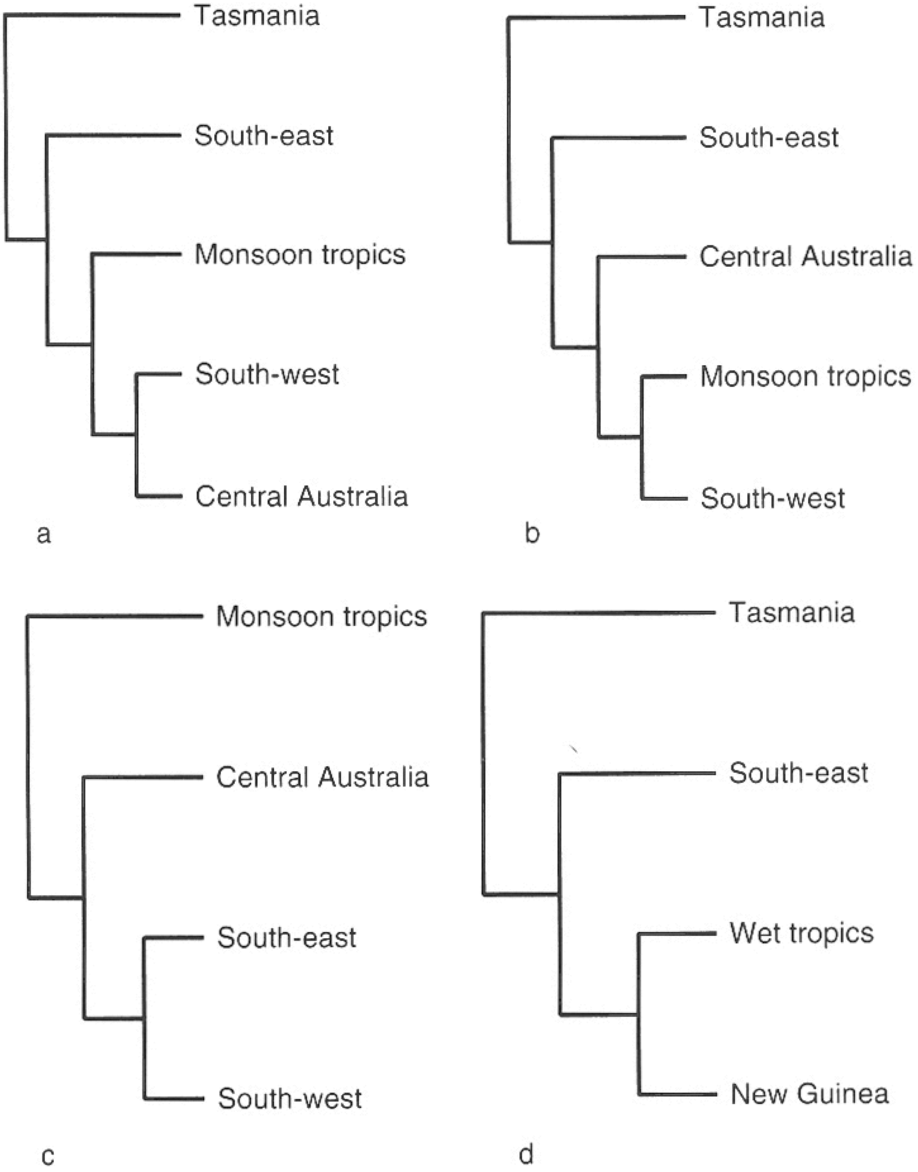

Figure 80. Four partial area cladograms for Australia. Each is a hand-built clique of combinable non-paralogous subtrees extracted from area-cladograms of Australian angiosperm taxa. None of the partial area cladograms except **(c)** and **(d)** can be combined, i.e. they conflict. **(a)**, *Daviesia latifolia* group, *Leptosema* (first subtree), *Cullen* (Fabaceae) and *Persoonia* (Proteaceae). **(b)**, as for **(a)** except that *Lechenaultia* (Goodeniaceae) is substituted for *Persoonia*. **(c)**, *Gossypium* (Malvaceae) and the second subtree from *Leptosema*. **(d)**, *Lomatia* and Embothriinae (Proteaceae).

South-west and South-east. Note that of the three possible relationships between Central Australia, the Monsoon tropics and the South-west, all three are represented in Fig. 80a–c. It seems surprising that *Leptosema* should include two conflicting subtrees. This may be due to uncertainty in the phylogenetic position of *L. oxylobioides*, which occurs in the South-east area (Crisp, 1998, in press). If this species is removed, then both subtrees from the genus agree with the clique in Fig. 80c. A fourth clique (Fig. 80d), based on the closely related taxa *Lomatia* and Embothriinae, follows quite a different track from the first three, since it includes the Wet tropics and New Guinea but does not include the Monsoon tropics, Central Australia and South West. Like the first two cliques, this track has Tasmania differentiating first, then the South-east, then the Wet tropics and New Guinea.

Interpretation

The differences among the four cliques tend to support the view that there is no unique phytogeographic history of areas within Australia. Instead there appear to be multiple tracks that overlap, at least partially. For example, the track shown by *Lomatia* and Embothriinae (Fig. 80d) has the same basal portion (Tasmania and the South-east) as tracks shown by two different cliques of taxa (Fig. 80a–b). That it is possible to identify cliques of combinable subtrees from different taxa suggests that these tracks may be general. If this is the case, then it should be possible to find subtrees from additional taxa which corroborate these tracks. Given the present state of knowledge, more definite conclusions cannot be drawn. However, some key problems can be identified:

(1) One of the most interesting results is that the Wet tropics seem to be more closely related to New Guinea than to other Australian areas. This is evidenced both by the proteaceous taxa *Lomatia* and Embothriinae (Fig. 80d) and by Sapindaceae (Turner, 1996). Both groups appear to belong to the South Pacific track (above), consistent with earlier suggestions that the Australian rainforests are a vicariant relic of ancient Gondwanan floras (Webb *et al.*, 1986; Schodde, 1989; Weston & Crisp, 1994). But it also raises the question of how internal Australian tracks relate to external tracks. If this track is indeed Gondwanan, then is the internal portion also Gondwanan, or post-Gondwanan? To answer this question, it will be necessary to find additional phylogenies of taxa which can differentiate areas both within and beyond Australia.

Cullen also is part of an external track, extending through Malesia to east Asia and west to the Mediterranean and Africa (Grimes, 1997). Other legume taxa share this track, e.g. *Crotalaria*, *Rothia* and *Cajanus*. Even though these are not rainforest taxa, they may be part of the equatorial track, since tracks are not limited to a particular habitat.

(2) Tasmania takes a basal position in the plant area-cladograms discussed here, but in Cracraft's (1991) analysis, its position varied among the fundamental area-cladograms from different taxa. Other plant taxa not discussed here (e.g. some eucalypts and genera of Fabaceae) appear to show a relatively more recent differentation of Tasmanian species. Ambiguities are to be expected in Tasmania's relationship to the mainland, since Bass Strait has been flooded and exposed repeatedly since Australia detached from Antarctica c. 40 Ma (BMR Palaeogeographic Group, 1990; White, 1994).

(3) There are conflicting hypotheses about how the central desert relates to the rest of Australia. Both Burbidge (1960) and Schodde (1989) hypothesised that the region was colonised by speciation of taxa occurring around the periphery of the continent, and that this occurred repeatedly during the wet-dry cycles from the late Tertiary until the present. Therefore, different arid-zone taxa would be expected to show different tracks varying both in age and in their connections to peripheral areas. This appears to be the case in our analyses of angiosperm taxa (Fig. 80a–c). By contrast, Cracraft's (1991) analysis of vertebrate taxa gave a single Central Australian track: all the desert areas were more closely related to each other than to any peripheral area (Fig. 79a). Both patterns may be real. It is possible that Cracraft included groups in his analysis that have radiated in the arid zone. It would be interesting to see whether an analysis of plants that are arid zone specialists, e.g. Chenopodiaceae or *Triodia*, would give a similar result.

(4) Another problem that has preoccupied many biogeographers of Australia (Hooker, 1860; Diels, 1906; Burbidge, 1960) is the temperate east-west relationship. Many characteristically Australian genera seem to follow a track between the South-east and South-west, with a strong disjunction across the Nullarbor Plain - few species are common to both areas. Examples are *Eucalyptus* (Myrtaceae), *Acacia* and most genera of the Mirbelieae (Fabaceae), *Banksia*, *Grevillea* and *Hakea* (Proteaceae), and *Boronia* (Rutaceae). Most of these have greater diversity in the west than in the east, and it has been speculated that the autochthonous flora originated in the South-west (e.g. Diels, 1906). The Nullarbor has been a barrier (marine, then edaphic and climatic) between east and west continuously since the early Tertiary (Nelson, 1981; BMR Palaeogeographic Group, 1990; White, 1994). Thus, it might be expected that the South-west would show early isolation from the South-eastern areas. While this appears to be the case in Fig. 79b, it is not evident in the subtrees (Fig. 80a–c). Further investigation of this south coastal track is needed.

Small-scale tracks: phylogeographic studies within species

Even at the lowest phylogenetic levels, i.e. within species, geographic patterning is evident. As the units of analysis are more recently evolved than species and supraspecific taxa, younger geographic patterns are expected. Also, as these taxa tend to be more restricted geographically than higher taxa, more local patterns (shorter tracks) are expected.

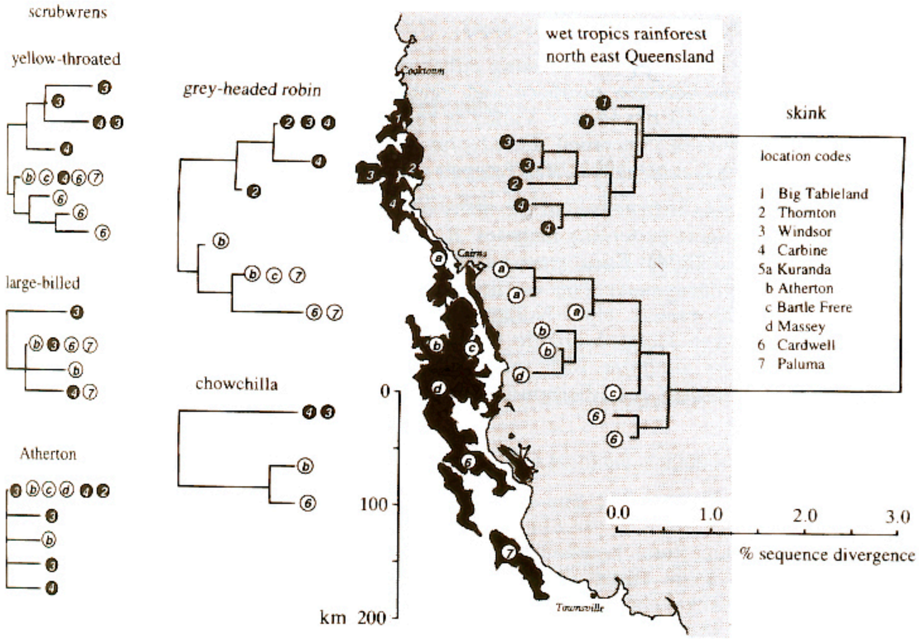

Figure 81. Geographic patterning of mitochondrial DNA (mtDNA) phylogenies within six vertebrate species from the tropical rainforest (wet tropics) of northern Queensland. Alleles from localities north of the Black Mountain Barrier (BMB) are shown as filled circles; those from south of the BMB are shown as open circles; letters and numbers refer to the locations marked on the map: locations 5a to 5d are all from the Atherton tableland. Phylogenies are drawn to scale. The shaded area within the map indicates the current distribution of rainforest. Note the congruent vicariance across the BMB in the skink, robin, yellow-throated scrubwren and chowchilla. Reproduced from Joseph *et al.* (1995) with permission.

In recent years improved molecular technology, as well as the apparent informativeness of unipaternally inherited genomes (chloroplast and mitchondrial DNA) at this level, has spawned a plethora of molecular studies under the neologism 'phylogeography' (Avise *et al.*, 1987). By their non-recombinant mode of inheritance these genomes always produce a hierarchical (phylogenetic) pattern among the samples. However, sexually reproducing organisms have reticulating (tokogenetic) relationships, and a phylogeny based on chloroplast or mitochondrial DNA alone can give a very misleading picture of organismal relationships (Melnick & Hoelzer, 1993; Doyle, 1995). Nevertheless if these limitations are borne in mind, the molecular data are useful, especially if multiple lines of evidence (nuclear, organellar and morphological) are used. Molecular data allow the possibility of dating events by use of a molecular clock, whose conditions are more likely to be satisfied among closely related organisms.

The most comprehensive phylogeographic studies to date in Australia have focussed on vertebrates in the wet tropics of northern Queensland (Joseph & Moritz, 1993, 1994; Joseph *et al.*, 1993, 1995; Moritz *et al.*, 1993). The authors used mitochondrial DNA to reconstruct infraspecific phylogenies of birds and lizards and found a congruent pattern (among species) of divergence between populations in northern and southern rainforest areas, which are separated by a dry area known as the 'Black Mountain Barrier'. Using a molecular clock, they hypothesised a vicariance event (or series of events) during the late Tertiary or Pleistocene, apparently caused by climatic fluctuations (Fig. 81). Their study area falls entirely within Schodde's (1989) Tumbunan element, which is the northern extension of our South Pacific track, and presumably their pattern reflects more recent substructuring of this ancient track. Corroboration of this pattern is now being sought from plant taxa, including Lauraceae (J.West, B.Hyland & L.Spindler, unpublished).

Farther south, three botanical studies using either molecular or morphological data revealed strong differentiation between northern and southern populations in the Great Dividing Range. For all three taxa the Hunter Valley is the barrier across which differentiation has occurred. These studies concerned *Eucalyptus dalrympleana* (Williams, 1991), *Acacia melanoxylon* (Playford *et al.*, 1993) and *Telopea speciosissima* (Crisp & Weston, 1993).

A sample (by no means exhaustive) of the many other such studies on species complexes that show distinct geographic patterning includes: *Blandfordia* in the Sydney region (Porter *et al.*, 1992; Ramsey *et al.*, 1994); *Eucalyptus baxteri* in Victoria and South Australia (Marginson & Ladiges, 1988); *Acacia suaveolens* on the east coast (Morrison & Rupp, 1995); *Cardamine lilacina* in the south-eastern alps (Nolan *et al.*, 1996); *Eucalyptus caesia*, which shows differentiation between isolated granite outcrops in the south-west (Hopper & Burgman, 1983); and *Daviesia ulicifolia* with many intergrading races from Cape York south to Tasmania and west to the Great Victoria Desert (Chandler & Crisp, 1998).

Conclusion

Australia is a unique floral kingdom with high endemism (above 80% at species level), relative to the rest of the world. Yet, at the higher taxonomic levels (family and above), it contains a representative sample of the world's flora. As first recognised by Hooker (1860), the Australian flora shows a complex web of affinities with the rest of the world. The closest relationships are with lands in the Southern Hemisphere, especially New Guinea, New Caledonia, New Zealand and southern South America. Track analysis and cladistic methods are beginning to tease out vicariant patterns (resulting from the break-up of Gondwana) from conflicting patterns due either to dispersal or to complex and poorly understood geological processes.

Previously Hooker has been misrepresented as proposing the 'invasion theory' adopted by later authors to explain the origins of the Australian flora. It is shown here that he was primarily concerned with identifying floristic affinities between distant geographic regions, analogous with the general tracks recognised by Croizat and in this review. If Hooker favoured any process explanation for trans-oceanic affinities, then it was vicariance of a once-contiguous ancestral flora.

Within the Australia-New Guinea craton, the flora is well-differentiated, allowing the recognition of several floristic 'elements' or regions by authors from Hooker to Schodde. A number of centres of endemism also have been recognised, of which the Wet Tropics in the north-east and the sclerophyll flora of the South-west are the most distinctive and diverse. These two centres contrast strongly in climate and vegetation and have almost no species in common. Such high diversity *between* areas accounts for the recognition of Australia as an area of endemism with global significance.

Efforts to trace general floristic tracks within the continent, and to find general phylogenetic relationships among areas, have not been very successful. This is probably due to the relative ease of dispersal within a continuous land-mass, thus obscuring evidence of vicariance. However, phylogeographic studies of species have shown evidence of recent vicariance events in the wet tropics of north-east Queensland and the Hunter Valley of New South Wales.

Acknowledgments

We thank Peter Cranston, Penny Gullan, Geoff Hope, Pauline Ladiges, Gary Nelson and Tony Verboom for useful comments on the manuscript, and Tony Orchard for contributions to the historical section.

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PRESENT VEGETATION TYPES

R.H.Groves[1]

Australian vegetation types are the result of interaction between a wide range of factors, some major, some minor. The most important determinant is rainfall, both its total amount and its distribution throughout the year: summer-incident in the north and winter-incident or all-year-round in the south. Closely related to rainfall as a determinant of vegetation type is temperature, which influences available water. Of lesser influence, but still often important at a regional or local level are such factors as soil type, drainage, nutrient level, salinity, grazing pressures, exposure and of course, fire, whether natural or human-induced. All of these factors act upon a flora which has been shaped over many millions of years by changing climates and geomorphology, as well as by evolution and recruitment from other regions. For details see chapters in this volume by Frakes (climate & geomorphology); Hill *et al*. (palaeobotany); and Crisp *et al*. (biogeography).

Several attempts have been made to classify and name Australian vegetation types. Aboriginal peoples recognised many associations and their terms for distinctive vegetation such as brigalow, kwongan, mallee, mulga and wallum have been taken into general parlance. Subsequent attempts, dating from the time of Banks in 1770, used more Europocentric terms, either in relation to some vegetation types (e.g. 'heath') or to some dominant genera, such as 'box'-barked eucalypts or 'wattles' (*Acacia* spp.). Some terms still in current use, such as 'dry' and 'wet' sclerophyll forests, add environmental descriptors to the terminology, which can be confusing.

More recent attempts to classify present Australian vegetation have usually been based on a mixture of structural and floristic attributes; such a mixture is still used and appropriate because of the predominance of *Eucalyptus*, the phyllodineous spineless group of *Acacia* species, and *Triodia* in many Australian plant communities. In those vegetation types where the above genera do not occur and in which there is high floristic diversity, e.g. some closed-forests, usually only structural attributes have been used (see e.g. Webb *et al*., 1976), although even here descriptions based on floristics have been used (e.g. in heath vegetation).

The system of classification most commonly used in Australia currently is the structural one of Specht (1970); it is a subsequent modification to this system (see Table 24) which is employed throughout most of this chapter. This simple system of a two-dimensional matrix uses life-form and foliage projective cover of the tallest stratum to characterise most major vegetation types. Specht's system, with the modification to it of the floristics of the over- or under-storey, has been used subsequently to successfully map Australian vegetation at both regional and continental scales (Beard, 1976; Carnahan, 1976, 1977, 1990) (Fig. 82).

This chapter describes the distribution across Australia of five major vegetation types — closed-forests (both tropical and temperate), open-forests, woodlands, shrublands and grasslands. The vegetation types in some regions of extreme conditions, such as alpine or coastal vegetation, will not be described except in passing (but see relevant chapters in Groves, 1994 for further detail). Regional patterns that operate at different scales to modify the distribution of these five major vegetation types over the continent are outlined towards the end of the chapter.

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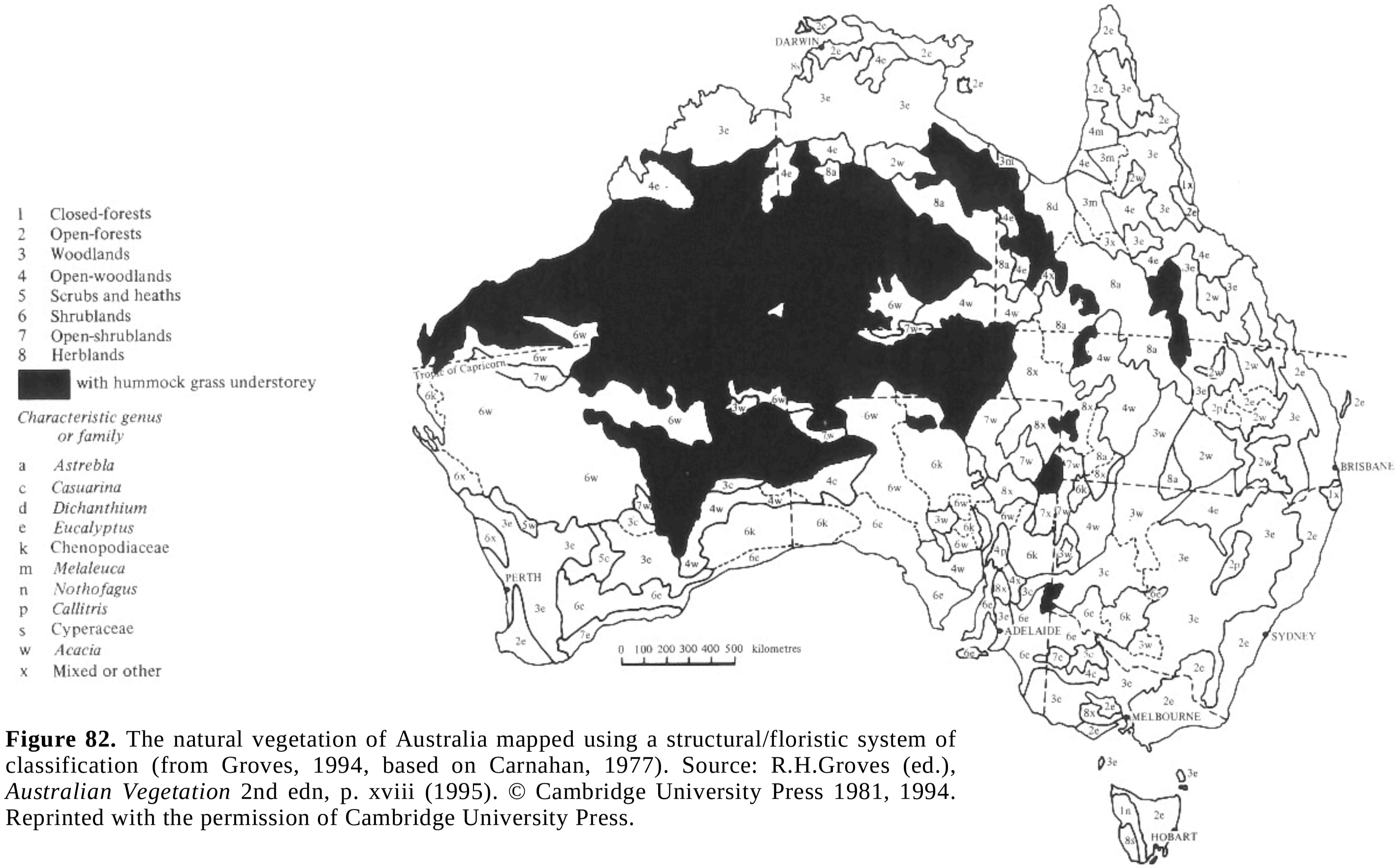

Figure 82. The natural vegetation of Australia mapped using a structural/floristic system of classification (from Groves, 1994, based on Carnahan, 1977). Source: R.H.Groves (ed.), *Australian Vegetation* 2nd edn, p. xviii (1995). © Cambridge University Press 1981, 1994. Reprinted with the permission of Cambridge University Press.

Table 24. Structural formations in Australia and their percentage area (adapted from Specht *et al*., 1974).

Life form and height of tallest stratum	Foliage projective cover of tallest stratum						
	100–70%		70–30%		30–10%	<10%	
Trees> 30m.	Tall closed-forest	0.92%	Tall open-forest 1.64%		(Tall woodland)	(Tall open-woodland)	
Trees 10–30 m.	Closed-forest		Open-forest	3.61%	Woodland 17.84%	Open-woodland	5.80%
Trees <10m	Low closed-forest		Low open-forest		Low woodland 4.81%	Low openwoodland	
Shrubs >2m	Closed scrub		Open scrub 7.69%		Tall shrubland 9.89%	Tall open-shrubland 0.22%	
Shrubs 25 cm–2m	Closed-heath		Open-heath 1.47%		Low shrubland 4.00%	Low open-shrubland 14.39%	
Shrubs <25 cm	–		–		Fell field	Open-fellfield	
Hummock grasses <2 m	–		–		Hummock grassland 3.95%	Open-hummock grassland 14.71%	
Graminoids, herbs, ferns, etc.	Closed-grassland		Grassland 1.13%		Open-grassland 6.69%	Ephemeral herbland	

Major vegetation types

Closed-forests (tropical and temperate rainforests)

In recent geological times, the total area of closed-forest, sometimes called rainforest, has been relatively small (less than 1% of the continental surface) and discontinuous. Pockets of closed-forest cover more than 30 degrees of latitude along the east coast, from Cape York to southern Tasmania (Fig. 83). Webb & Tracey (1994) referred to these pockets as 'islands' in a 'sea' of sclerophyll vegetation, which follows Herbert's earlier analogy of an 'archipelago of habitats' (Herbert, 1967). Such a pattern of discontinuity and fragmentation of closed-forest types is more pronounced in the drier inland areas of northern Australia (Webb & Tracey, 1994) and in closed-forests ('temperate rainforests') in southern Australia (Busby & Brown, 1994).

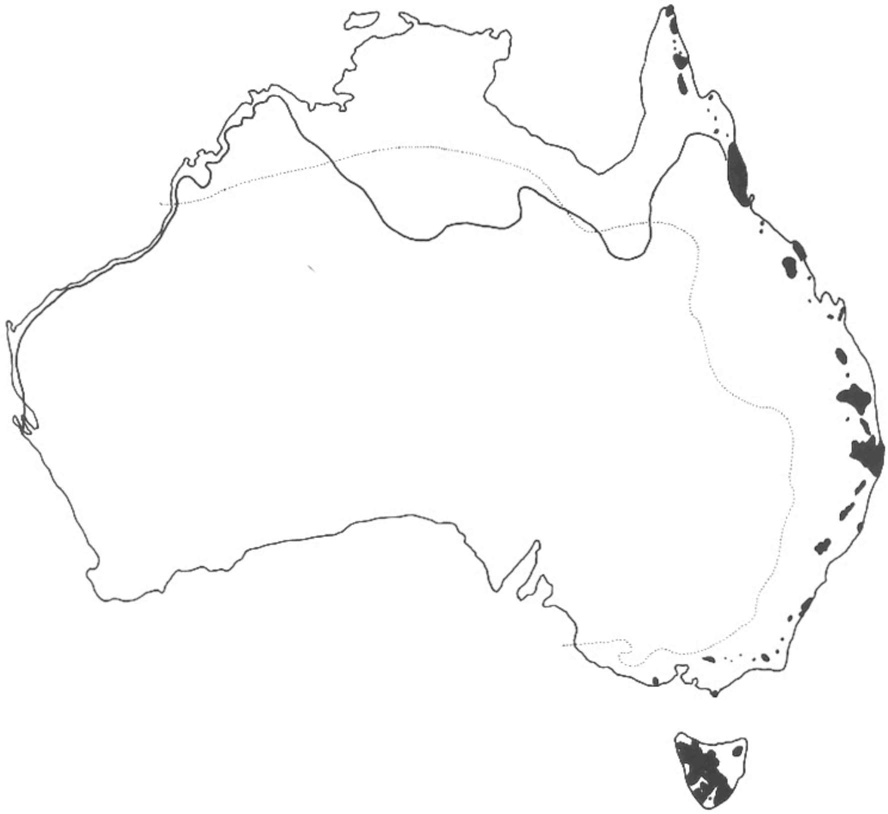

Figure 83. Distribution of Australian closed-forest types. Shaded area = rainforest; dotted line = 800 mm rainfall isohyet; solid line = limit of closed vine thickets. Redrawn (P.McCarthy) from L.J.Webb & J.G.Tracey, The rainforests of northern Australia, *in* R.H.Groves (ed.), *Australian Vegetation* fig. 4.1 (1994).

Wherever closed-forests occur, and however discontinuous and fragmented their distribution may be, they always have a closed canopy (greater than 70% foliage projective cover; see Table 24) with trees densely spaced. Closed-forests in tropical climates are characterised by a complex mixture of species (Figs 5, 6, 7, 23) with no one species or genus dominant and usually an array of certain life-forms, such as angiosperm epiphytes, lianes and trees with buttresses (see Fig. 84 for a profile through a sample of a type of closed-forest called 'simple

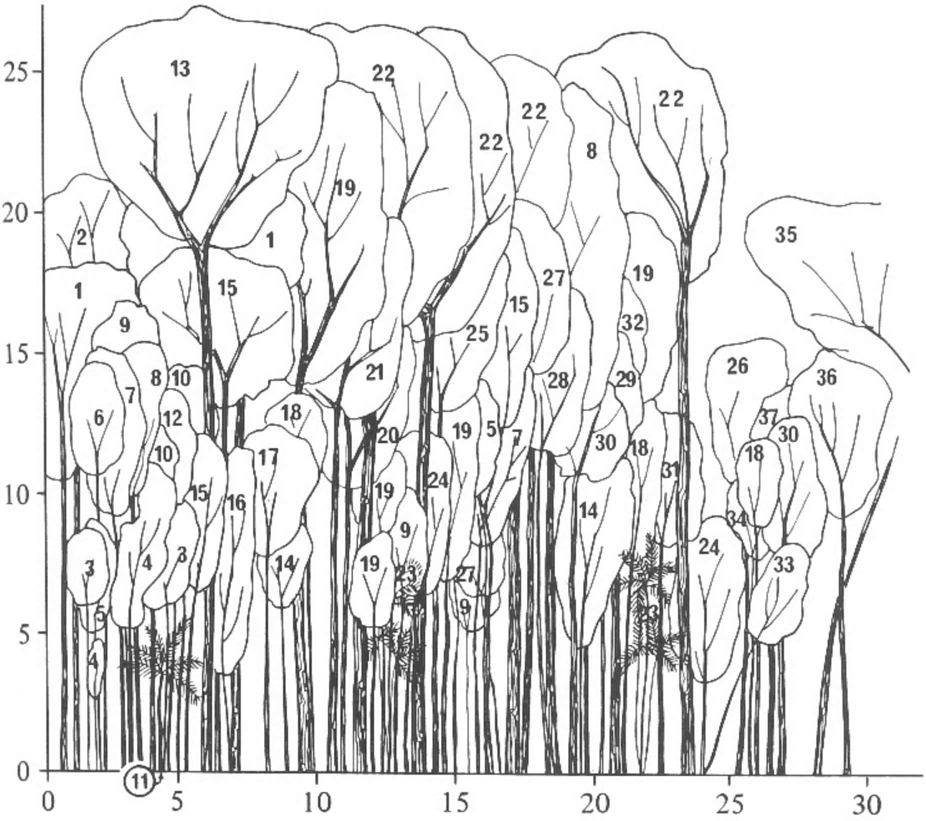

Figure 84. A profile diagram illustrating a simple notophyll vine-fern forest, a structural type of tropical closed-forest. 1. *Elaeocarpus largiflorens*; 2. *Polyscias murrayi*; 3. *Pullea stutzeri*; 4. *Rhodomyrtus trineura*; 5. *Apodytes brachystylis*; 6. *Opisthiolepis heterophylla*; 7. *Cryptocarya densiflora*; 8. *Ceratopetalum virchowii*; 9. *Sarcopteryx martyana*; 10. *Cryptocarya corrugata*; 11. *Orania appendiculata*; 12. *Cinnamomum laubatii*; 13. *Prumnopitys ladei*; 14. *Rapanea achradifolia*; 15. *Carnavonia* sp.; 16. *Guettardella tenuiflora*; 17. *Syzygium endophloium*; 18. *Acmena hemilampra* spp. *orophila*; 19. *Sphalmium racemosum*; 20. *Endiandra montana*; 21. *Symplocos cyanocarpa*; 22. *Flindersia pimenteliana*; 23. *Laccospadix australasicus*; 24. *Rhodamnia blairiana*; 25. *Garcinia brassii*; 26. *Syzygium cormiflorum*; 27. *Planchonella obovoidea*; 28. *Cryptocarya angulata*; 29. *Diospyros* cf. *hemicycloides*; 30. *Goniothalamus australis*; 31. *Beilschmiedia collina*; 32. *Sphenostemon lobosporus*; 33. *Wilkiea macooraia*; 34. *Aceratium ferrugineum*; 35. *Alphitonia petriei*; 36. *Planchonella macrocarpa*; 37. *Elaeocarpus stellularis*. Source: L.J.Webb & J.G.Tracey, The rainforests of northern Australia *in* R.H.Groves (ed)., *Australian Vegetation*, 2nd edn, fig. 4.6d (1994). © Cambridge University Press 1981, 1994. Reprinted with the permission of Cambridge University Press and the authors.

notophyll vine-fern forest'; Webb & Tracey, 1994). On the other hand, the southern closed-forests that occur at either higher latitudes or altitudes in climates characterised by frequent frosts and some snow are simpler floristically, with the Gondwanan genus *Nothofagus* dominant, although several other genera may also be dominant locally. The southern closed-forests are distinguished from their tropical counterparts by the absence of significant buttressing at the tree bases and lack of woody lianes. Epiphytes in southern closed-forests are mainly ferns, bryophytes and lichens with only two species of epiphytic angiosperms (Busby & Brown, 1994).

Visually striking sharp boundaries usually separate closed-forests from the adjoining and more widespread sclerophyll vegetation. Sometimes, however, such edges between the two vegetation types may be diffuse, depending on fire characteristics and history. Most closed-forest species are evergreen, although some winter-deciduous species may occur, especially in dry northern sites.

Classification of the different sub-types of closed-forests has resulted in an enhanced understanding of the ecological factors that may control their distribution. Such classification has also established a more rational basis for a system of reservation of different types of closed-forest in eastern and northern Australia (Webb *et al.,* 1973) and Tasmania (Brown *et al.,* 1990).

Based largely on numerical analyses of floristic data collected over the entire latitudinal range of distribution, Webb & Tracey (1981) subdivided closed-forests into many types. These floristic types, at the species level, could be correlated with climatic types, such as 'tropical wet', 'tropical dry' and 'subtropical and temperate wet' provinces, but at the generic level no such correlation was possible (Webb *et al.,* 1984; Webb & Tracey, 1994). While similar floristic subdivisions are possible in southern closed-forest (e.g. that between *Nothofagus* and *Athrotaxis* alliances in Tasmania; Busby & Brown, 1994), most analytical effort has been in northern closed-forests, and especially in the canopy species of those forests, because of their greater floristic diversity at the species level. To illustrate this floristic difference, Beadle (1981) cited data from one site in north-eastern Queensland with 105 tree species listed in the upper canopy, of which 77 were found only in one plot, 15 occurred in two plots and only 1 tree species occurred in more than 5 plots, each plot being 0.5 ha. This floristic richness contrasts with the situation in southern closed-forests in which the canopy may comprise no more than 3 or 4 species, while occasionally there is only one (Busby & Brown, 1994).

The complex classifications developed by the workers above reflect the latitudinal and climatic range over which closed-forest is found, and the taxa of which they are composed. The taxonomic content of closed-forest is not uniform in number or in content, nor is it entirely clinal, however. Closed-forest communities contain a number of centres of species richness and endemism, particularly in the Cape Tribulation and Atherton Plateau areas of Queensland, the 'Macleay-McPherson Overlap' region on the border of Queensland and New South Wales, and in Tasmania.

The floristic composition of the closed forests of the north-eastern Queensland region (Figs 5, 9) have often been compared to (or even thought to be derived from) those of Indo-Malaya. This view, however, has been contested by the results of more recent work which suggests that many of the taxa in these communities are derived from an ancient Gondwanan flora (Webb *et al*., 1986; Truswell *et al*., 1987; Barlow & Hyland, 1988). The north-eastern closed-forests contain a number of 'primitive' Magnolialian and Lauralian groups such as *Bubbia* and *Tasmannia* (Winteraceae), *Galbulimima* (Himantandraceae), *Eupomatia* (Eupomatiaceae), *Austrobaileya* (Austrobaileyaceae) and *Idiosperma* (Idiospermaceae). Vines are common, particularly in the lowlands, and include *Flagellaria indica*, *Rhaphidophora* spp., *Bambusa moreheadiana*, *Smilax* spp., *Faradaya splendens*, and climbing palms such as *Calamus* spp. Arborescent palms (Arecaceae) such as *Archontophoenix alexandrae*, *Licuala ramsayi*, *Orania appendiculata* and *Linospadix* spp. are common emergents or subcanopy taxa. Epiphytic ferns such as *Asplenium* spp., (Fig. 7) and *Platycerium* spp., orchids such as *Dendrobium* spp. and *Bulbophyllum* spp. and strangling figs (*Ficus*) are also abundant. Canopies and sub-canopies contain a range of endemic or near endemic tree genera, including *Doryphora* (Monimiaceae), *Ceratopetalum* (Cunoniaceae), *Darlingia*, *Cardwellia*, *Buckinghamia*, *Musgravea* (all Proteaceae), *Backhousia* and *Lindsayomyrtus* (Myrtaceae) and *Blepharocarya* (Anacardiaceae), and other more widespread genera like *Castanospermum* (Fabaceae). The gymnosperms *Araucaria* spp. (Fig. 10) and *Agathis* spp. are distinctive emergents in places (Beadle, 1981; Busby & Brown, 1994).

Further south, the numbers of vines, palms and epiphytes progressively decreases. In New South Wales the closed-forests are often dominated by *Doryphora sassafras* (Monimiaceae) and *Ceratopetalum apetalum* (Cunoniaceae). In some areas other species such as *Acmena smithii*, *Tristania laurina*, *Syzygium* spp. (all Myrtaceae), *Argyrodendron* spp. (Sterculiaceae) and various taxa of Lauraceae, Simaroubaceae, Rutaceae, Meliaceae and *Nothofagus* spp. may be major components (Beadle, 1981, Busby & Brown, 1994).

The cool temperate closed-forests of Tasmania are largely dominated by *Nothofagus cunninghamii* (Figs 11–14). In western Tasmania this species may form virtually monospecific forests with a sparse understorey of terrestrial ferns. More commonly it forms a mixed canopy with *Atherosperma moschata* (Atherospermataceae) and *Phyllocladus asplenifolius* (Podocarpaceae), with a range of genera such as *Eucryphia*, (Eucryphiaceae) *Anodopetalum* (Cunoniaceae), *Cenarrhenes*, *Agastachys*, *Orites*, *Telopea* (all Proteaceae), *Richea* (Fig. 15), *Archeria*, *Cyathodes* (all Epacridaceae), *Anopterus* (Grossulariaceae), *Pittosporum* (Pittosporaceae) and *Tasmannia* (Winteraceae) represented in the understorey. A more restricted closed-forest type is that dominated by *Athrotaxis cupressoides* (Cupressaceae), found only at high-altitude sites (Fig. 16) (Busby & Brown, 1994; Read & Brown, 1996).

Open-forests

Open-forests are a much more diverse group of vegetation types, occupying between 5% and 14% (depending on definition) of Australia in pre-European times. They are defined as those forest types with between 30% and 70% foliage projective cover of the dominant stratum and range from tall open-forest (>30 m tall) to open-heath (25 cm to 2 m tall). Pre-European Australian vegetation was made up of about 1.64% tall open-forest, 3.61% medium to low open-forest, 7.69% open-scrub and 1.47% open-heath (Specht *et al*., 1974). Open-forests are found mainly in a coastal band up to 250 km wide extending from near Darwin in the north around the east coast to the vicinity of Melbourne, with isolated pockets extending further inland in southern Queensland, in the eastern half of Tasmania, and in south-western Western Australia (Fig. 82).

In higher rainfall areas of eastern Australia open-forest species rely on some particular frequency or intensity of fire to maintain their dominance, and it is this which determines whether a particular area remains as open-forest or closed-forest. For example, in parts of Tasmania a fire occurring more frequently than once in about every 400 years will maintain the dominant eucalypts and exclude dominance of closed-forest species such as *Nothofagus cunninghamii* (Gilbert, 1959; Howard, 1973, 1981; Busby & Brown, 1994). Fire frequencies of between about 80 and 400 years may lead to a 'mixed' forest of *Eucalyptus*-dominated tall open-forest and other communities in which closed-forest floristic elements will be present to varying degrees in the understorey, such as can be found in moist areas of southern Victoria and Tasmania (Busby & Brown, 1994).

Another common feature of open-forests is the omnipresence of species of eucalypts in the upper stratum of such forests (*Eucalyptus s. lat.* was recently divided by exclusion of the bloodwoods as the genus *Corymbia* (Hill & Johnson, 1995). The vernacular descriptor 'eucalypts' is still usually applied to *Eucalyptus s. str*. + *Corymbia* + (sometimes) *Angophora*), however. A mixture of two or more species from different subgeneric groups of *Eucalyptus* may dominate some open-forests (Florence, 1981). Ashton & Attiwill (1994) commented aptly that tall open-forests 'are the supreme expression of the genus *Eucalyptus sensu lat*.'. Other genera, however, may be dominant in some open-forests. In some coastal open-forests, such as those near Sydney, *Angophora* species may be codominant. *Acacia* species, such as *A. harpophylla*, may form open-forests in south-eastern Queensland; they will be described briefly below (see Johnson & Burrows (1994) for further detail).

Many open-forest types have been recognised in both tropical and temperate Australia, depending primarily on tree height and species composition (Beadle, 1981; Ashton & Attiwill, 1994). Generally, subcategories of open-forests may be differentiated on the height of the dominant tree layer: as either tall (>30m), medium (10–30m) or low (>10m), but always with a foliage projective cover of between 30 and 70% (Table 24). While some closed-forest species may occur as an understorey to the eucalypt canopy, more usually the understorey species are shrubs or small trees with or without a ground stratum of grasses and/or ferns and mosses. Leaves of the understorey shrubs in tall open-forest are usually mesomorphic compared with the more xeromorphic leaves typical of the understorey species of lower forests. Tall open-forests generally occur in areas of higher rainfall and on soils of relatively higher fertility than the open-forests of medium or low heights, although there are local exceptions depending on fire history, substrate and microclimate.

While the distribution of closed-forests is confined to the more humid areas of eastern, and to a lesser extent, northern Australia, that of open-forests includes not only eastern and southern Australia, but also a relatively well-watered triangle between Perth and Albany in south-western Western Australia (Fig. 82). Though the same structural vegetation type occurs in the two regions, there is nonetheless a marked floristic discontinuity between the eucalypt species dominant in Western Australia and those in the east. It is some of these species dominant in tall open-forests in either region (Mountain Ash, *Eucalyptus regnans*, in south-eastern Australia; Karri, *E. diversicolor*, and Jarrah, *E. marginata*, in south-western Australia) which are among the tallest trees of the world; they can exceed 80 m (Ashton & Attiwill, 1994). What is more, in the case of *Eucalyptus regnans*, half of this final mature height may be achieved in the first 25 to 35 years following fire (Ashton & Attiwill, 1994).

Open-forests may be subdivided into different floristic types depending on either the species of *Eucalyptus* which dominates the tallest stratum (Beadle, 1981) or on the dominant species in the understorey. Ferns provide a pertinent example. In eastern Australia tree ferns of the genera *Cyathea* (Cyatheaceae) and *Dicksonia* (Dicksoniaceae) are often present in tall open-forests and may dominate the understorey, although they never occur in analogous south-western forests. Ground ferns may occur in the understoreys of both regions, however. A further floristic difference between the open-forests of east and west is the absence of closed-forest species in the lower strata of Western Australian tall open-forests.

The eucalypt species characteristic of the canopy of tall open-forests are usually fire-sensitive and lack a lignotuber; they regenerate as a cohort of even-aged seedlings from canopy-stored seed under the conditions of high light, high nutrient availability and changed soil microflora that inevitably follows a fire of high intensity. Only in the understorey species of tall forests are lignotubers represented, for example, in *Olearia argophylla* and *Bedfordia arborescens* (both Asteraceae), which also store their seed in the soil. On the other hand, eucalypts characteristic of open-forests of medium or low height generally possess lignotubers and their canopies may recover from fire by development of buds located on either the lignotuber or as epicormic buds beneath the generally thicker bark of the bole and major branches. Such forests may be much more 'mixed' in terms of age classes, as well as in species composition, than their taller counterparts.

Beadle (1981) recognised 10 alliances of eucalypt communities in the tropics, 10 alliances of tall eucalypt forests in the eastern coastal lowlands, 7 alliances of eucalypt woodlands and forests on soils of low fertility, mainly on the eastern coastal lowlands, 18 alliances of eucalypt communities of cooler climates of the eastern highlands, lowland Victoria and Tasmania, 4 alliances of Ironbark forests and woodlands of the east (Cape York Peninsula to Victoria), 13 alliances of Box woodlands of the east and south-east, 18 alliances of mallee and marlock communities, and 11 alliances of eucalypt forests and woodlands in the south-west, a total of 91 alliances. Most of these had a number of sub-alliances. It is therefore very difficult to generalise about floristic and ecological characteristics.

Very tall open-forests are found in two widely disjunct areas: the relatively wet margins of closed forest communities in south-eastern Australia (Victoria and Tasmania) (Figs 17, 18), and in south-western Western Australia in those areas where soil of good texture and reasonable fertility exists. The south-eastern forests, dominated by *E. regnans*, occur on rich, well-drained loamy soils, and reach heights of up to 90 m. They are fire-sensitive and thus tend to occur in stands of even-aged trees. Little or no eucalypt recruitment occurs in the understorey, because of low light levels. Instead, a sparse to moderately dense understorey of shade-tolerant shrubs and small trees such as *Bedfordia salicina* (Fig. 17), *Olearia argophylla*, (both Asteraceae), *Pomaderris apetala* (Rhamnaceae) and some *Acacia* species (e.g. *A. melanoxylon*). Tree ferns, particularly *Dicksonia antarctica* may be locally abundant (Fig. 18), and ferns of shorter stature such as *Blechnum* (Blechnaceae), *Histiopteris* and *Hypolepis* (both Dennstaedtiaceae), sedges and rushes may also be common. A successional shift in these very tall open-forests towards closed forest communities may occur over time, as such species as *Nothofagus cunninghamii* establish and replace smaller shrubs. Fire frequencies of less than 50–100 years favour *E. regnans*, frequencies of more than 350 years favour succession to closed-forest (Gilbert, 1959). The influence of fire is discussed in more detail later in this chapter. In the south-west of Western Australia the lack of tree ferns and adjacent closed-forest communities give the very tall forests a different facies. The tallest communities (Karri, *E. diversifolia*) grow to 70–85 m tall, with an often dense understorey of mesomorphic or semi-xeromorphic shrubs 3–7 m tall. The dominant understorey shrub is often *Trymalium spathulatum* (Rhamnaceae), with various species of *Acacia, Paraserianthes,* (both Mimosaceae), *Allocasuarina* (Casuarinaceae), *Agonis* (Myrtaceae), *Banksia, Persoonia* (both Proteaceae), Rutaceae, and Fabaceae (Beadle, 1981; Beard, 1990).

The medium to tall open-forests on both sides of the continent present superficially similar appearances. With varying degrees of fire-tolerance, they tend to be more mixed-age, and this provides a better-lit forest floor than the very tall forests (Figs 4, 19, 20). Consequently the understorey tends to be more diverse, and varies locally with conditions of water, light, nutrients, disturbance, fire frequency and other factors. Understorey shrubs come particularly from the Proteaceae (e.g. *Persoonia*, *Grevillea*, *Hakea*, *Banksia*, *Dryandra*), Fabaceae (e.g. *Pultenaea*, *Daviesia*, *Bossiaea*, *Gompholobium*), Myrtaceae (e.g. *Leptospermum*, *Agonis*, *Melaleuca*), Casuarinaceae (*Casuarina*, *Allocasuarina*), and Mimosaceae (*Acacia*) (Beadle, 1981; Beard, 1990).

Floristic composition of the understorey in medium and low open-forests is complex. Gill (1994) noted that there are numbers of genera which are common to both eastern and western Australia, such as shrubs of *Acacia* (Mimosaceae), *Daviesia* (Fabaceae), *Hakea* (Proteaceae), *Hibbertia* (Dilleniaceae), *Leptospermum*, *Leucopogon* (Epacridaceae) and *Pultenaea* (Fabaceae), the herbaceous genera (all rhizomatous) *Dianella* (Liliaceae), *Lepidosperma* (Cyperaceae) and *Lomandra* (Xanthorrhoeaceae), and the ferns *Adiantum* (Adiantaceae) and *Pteridium* (Dennstaedtiaceae). Furthermore, there are numerous discontinuities in species distributions between eastern and western open-forest floras, especially within the Orchidaceae (Green, 1964). There are also some obvious species disjunctions within eastern Australia, for instance on either side of Bass Strait.

The open-forests of Australia are complex floristically and ecologically. The predominance of *Eucalyptus* in all these open-forest types imparts a superficial uniformity to what is really a complex of vegetation associations and species which are often subtly adapted to local conditions. Interactions of soil types, patterns of water use and fire regimes are only recently coming to be understood for some open-forest types. Much still needs to be learned about this 'important and conspicuous element of the Australian landscape' (Gill, 1994: 219).

Woodlands

The foliage projective cover of Australian woodlands varies widely from 0.1 to 70 per cent; such woodlands may also vary in height but they are always over 2 m tall (Table 24). Defined in this way, woodlands cover about 25 per cent of Australia, in a band of varying width (up to 500 km) on the 'arid' (usually inland) side of the open-forest communities, and extend northwards into southern Papua New Guinea. They occur in all mainland Australian States and Territories, and on the Bass Strait Islands, but are rare in Tasmania (Fig. 82). They are dominated by perennial woody plants, usually of the genera *Eucalyptus* and *Acacia* (Figs 21, 22, 24, 25, 27, 100, 104) but occasionally of *Melaleuca* (Myrtaceae), which do not have their crowns touching; usually they have a grassy understorey (Gillison, 1994). Because of the latter characteristic, they have sometimes been referred to as 'savanna' woodlands in the past.

Of the c. 700 species of eucalypts so far described, about 80 per cent of them occur in woodlands (Gillison, 1994). In northern Australia where annual rainfall is less than 600 mm *Acacia* spp. tend to replace eucalypts. *Melaleuca* spp. may dominate woodlands in areas where seasonally fluctuating watertables are pronounced (Figs 8, 26). While the majority of woodlands are evergreen, some of the northern woodlands have genera present in the overstorey which may be winter-deciduous. These genera include *Terminalia* (Combretaceae) and *Bauhinia* (Caesalpiniaceae).

Woodlands are characterised not only by the form and spacing of the dominant trees but also by the presence of a grassy understorey, in contrast to the sclerophyll shrub understoreys typical of most open-forests. The grassy understorey of such woodlands has undergone considerable floristic change over the last 200 years in many regions. Such changes have arisen primarily because of the effects of continuous grazing by introduced animals, with often complex interactions between grazing and changed fire regimes, nutrient enrichment and plant species introductions, leading to a diversity of understorey types. The understorey to some woodlands, such as those in south-eastern Australia dominated by *Eucalyptus melliodora,* is now composed nearly entirely of annual species of Mediterranean origin, because few indigenous species can persist under such a continuous grazing regime (Table 25) (Moore, 1970). In this instance, even the dominant eucalypts fail to regenerate unless protected from grazing and the entire plant community disappears, as has happened over large areas of central New South Wales and northern Victoria.

In terms of surface soil nutrients, woodlands are usually less impoverished than the adjoining open-forests with a sclerophyll shrub understorey. The corollary to this difference is that, about 200 years ago, not only did such woodlands have a grassy understorey suitable for grazing, but they were initially easier to clear and more productive to graze; the resultant changes in understorey composition were accordingly greater. Remnants of the original understorey flora now exist in only a few cemeteries or roadside verges in southern Australia. Similar changes to the understoreys of northern Australian woodlands have occurred more recently as they are utilised increasingly for grazing.

A unique type of vegetation in southern Australia known as 'mallee' may be both a tall shrubland or a low woodland; as such, it sits between the broad subdivisions of woodland and shrubland used in this chapter. The word 'mallee' is an Aboriginal term for a eucalypt with lateral roots close to the soil surface from which drinking water could be obtained. Mallee vegetation is dominated by mature eucalypts which possess not only water-yielding roots but also a strongly developed lignotuber that develops at the base of the main stem. From this lignotuber arise numerous stems of more or less equal size, either as part of the inherent growth form, or as the result of sprouting of buds from the lignotuber when the main stem loses apical dominance as a result of drought, fire, frost or herbivore damage. (Figs 28, 99). Depending on the height of the regrowth, a woodland or a tall shrubland results. The same vegetation dominated by certain eucalypts, such as *Eucalyptus oleosa*, has been mapped as either woodland or shrubland by different individuals and provides one reason why the all-encompassing aboriginal term has been retained.

Different types of mallee vegetation are usually characterised by the taxonomic identity of the multi-stemmed eucalypt species (see, e.g. Noble & Bradstock, 1989; Parsons, 1994). Of the total number of *Eucalyptus* species described, about one fifth are mallees, with the greatest number occurring in south-western Western Australia (Parsons, 1994). What is more, the extent to which the multi-stemmed character is expressed in response to adverse site factors varies within a species, so that the same eucalypt taxon may have mallee and non-mallee forms (e.g. *Eucalyptus cladocalyx*). In semi-arid Western Australia vegetation occurs which is characterised by low single-stemmed eucalypts similar to mallees but which lack or have only a poorly developed lignotuber; these eucalypts are termed 'marlocks' – another

Table 25. Species changes resulting from grazing in herbaceous communities of *Eucalyptus melliodora–E. blakelyi* woodlands of the Southern Tablelands of New South Wales (after R.M.Moore (1970), with names updated).

Themeda triandra-Austrostipa aristiglumis-Poa caespitosa s. lat.

(Tall warm-season perennial tussock grasses)

GRAZING

↓

Austrostipa arisriglumis-Poa caespitosa s. lat. -Austrosripa scabra subsp. *falcata*

↓

Austrostipa scabra subsp. *falcata-Austrodanthonia carphoides-Austrodanthonia auriculata*

(Short cool-season, perennial grasses)

↓

Austrodanthonia carphoides-Austrodanthonia auriculata

(Short cool-season perennials)

↓

INTRODUCTION OF NATIVE SPECIES FROM MORE ARID COMMUNITIES

Enneapogon nigricans, Chloris truncata,

Tripogon loliiformis, Panicum effusum,

Vittadinia triloba, Euphorbia drummondii,

Convolvulus erubescens

(Short warm-season species)

GRAZING

↓

Austrodanthonia carphoides-Austrodanthonia auriculata

|

INTRODUCTION OF MEDITERRANEAN ANNUALS

Trifolium glomeratum, Vulpia bromoides,

Bromus spp., Hordeum leporinum,

Asreraceae, Erodium cicutarium,

Aira caryophyllea

(Exotic cool-season annuals)

|

Enneapogon nigricans, Chloris truncata, Panicum effusum,

Vittadinia triloba, Eragrostis brownii

(Short warm-season perennials)

GRAZING AND SUPERPHOSPHATE

↓

Vulpia bromoides, Bromus diandrus, Erodium cicutarium, Trifolium glomeratum, Cirsium vulgare

(Exotic cool-season annuals)

|

Chloris truncata, Eragrostis cilianensis, Chenopodium carinatum, Polygonum aviculare

(Warm-season species)

(Parameters: — Soils: Solodised solonetz. ph 5.9 (1:5 suspension). Rainfall: 584 mm per annum, distribution uniform. Altitude: 610 m above sealevel)

Aboriginal term still in use to describe a regional vegetation type. The genera *Acacia*, *Casuarina/Allocasuarina* and *Callitris* may be co-dominant with *Eucalyptus* in some areas of mallee vegetation.

The understorey to mallee vegetation may comprise either the sclerophyll shrubs or the chenopod shrubs to be described in the next section. In other cases, the understorey is more sparse and ephemeral with a high cover of litter and/or bare ground. In yet other cases, the hummock grass genus *Triodia* may characterise the understorey.

While mallee vegetation is typical of a large part of semi-arid southern Australia, the subalpine woodlands in the high-rainfall, montane areas of south-eastern Australia have the same form and structure (Williams & Costin, 1994). Just as mallee vegetation tends to be the most arid of the eucalypt-dominated communities of temperate Australia (but see Parsons, 1981, for some exceptions), so the subalpine woodlands are the most cold-tolerant of the tree communities; beyond the treeline in colder sites the woodland trees with a mallee form are replaced by alpine shrublands or grasslands. Subalpine woodlands of south-eastern mainland Australia are dominated by *Eucalyptus* species (particularly *E. niphophila* and *E. pauciflora*). In Tasmania other *Eucalyptus* species such as *E. coccifera* and *E. subcrenulata* form the treeline, often in association with or replaced by gymnosperms such as *Athrotaxis cupressoides*, *A. laxifolia*, *A. selaginoides* (Cupressaceae) and *Phyllocladus lawrencii* (Podocarpaceae), temperate rainforest stragglers such as *Nothofagus cunninghamii*, *Anopterus glandulosus*, *Persoonia gunnii* and *P. muelleri*, and some specialist subalpine taxa such as *Richea pandanifolia*, *R. scoparia* (Epacridaceae) and *Nothofagus gunnii* (Fagaceae).

A similar blurring of the distinction between low woodland and tall shrubland is evident for some vegetation dominated by *Acacia*, as occurs for analogous eucalypt-dominated mallee vegetation. Species of *Acacia* dominate some low woodlands and tall shrublands (and even some open-forests) in all regions of Australia generally too dry to support eucalypts (Johnson & Burrows, 1994). Some *Acacia* woodlands may also occur in more mesic areas, such as the *Acacia harpophylla* (brigalow) woodlands of south-eastern and central Queensland (Fig. 24). In general, the *Acacia* species characteristic of more arid regions, e.g. Mulga, *A. aneura* (Figs 104, 105) cope with water stress both physiologically and anatomically (e.g. by having photosynthetic phyllodes instead of leaves; thickened cuticles, etc) as well as by spatial patterning of the vegetation, whereby the *Acacia* occurs in thickets that receive run-off water from the sparsely vegetated inter-thicket areas (Johnson & Burrows, 1994). In general, different species, and even different Sections of the genus *Acacia*, occur in the canopy of woodlands on different soil types, but with past history also having an effect on species distributions (see Johnson & Burrows, 1994, for further detail). The complexities in patterning in *Acacia* species in semi-arid and arid regions rival that in *Eucalyptus* species characteristic of woodlands in more mesic Australia.

Other low woodland or tall shrubland communities are dominated by genera such as *Banksia* (Proteaceae), *Callitris* (Cupressaceae) and *Casuarina/Allocasuarina* (Casuarinaceae). *Banksia* woodland/tall shrubland is particularly well developed on parts of the coastal sand plain north of Perth, where *Banksia menziesii* and *B. attenuata* dominate woodlands and scrub heaths. Woodlands 4.5–6 m tall, dominated by *B. ashbyi*, are found fringing the arid zone from Freycinet Estuary to the Murchison River area. On the southern coastal sandplain of Western Australia, various *Banksia* species are major components of shrub-heaths, and near the coast *B. grandis* and *B. ilicifolia* may locally form woodlands or dense scrubs to 2–3 m tall (Figs 3, 103) (Beadle, 1981; Beard, 1990). In the east, species such as *B. serratifolia*, *B. aspleniifolia*, *B. robur* and *B. ericifolia* form similar coastal assemblages in Queensland and New South Wales, either as dominants or co-dominants with species of *Leptospermum*, *Casuarina/Allocasuarina*, and other taxa. *Callitris*, particularly *C. glaucophylla*, forms woodlands of limited extent in mallee regions of southern Australia, extending into central Australia (Fig. 21). In the tropics *C. glaucophylla* is replaced by *C. intratropica*, and in Western Australia the related genus *Actinostrobus* fills a similar niche (Beadle, 1981; Beard, 1990). Like *Callitris*, species of *Casuarina* and *Allocasuarina* are common components of eucalypt woodland almost throughout the country. In some areas they may form pure stands, as for example, woodlands of *Casuarina cristata* and *C. glauca* in eastern Queensland and New South Wales, *C. equisetifolia* in tropical coastal areas, and *Allocasuarina verticillata* in south-eastern Australia (Wilson & Johnson, 1989).

Shrublands

In Australia, two main types of shrublands have been recognised. Sclerophyll shrublands contain the same or similar species to those which comprise the understorey to open-forests of medium or low height (see above). This sclerophyll shrubland type is usually called 'heath' (Specht, 1994) but in Western Australia the Aboriginal term 'kwongan' has been used (Figs 3, 103) (Pate & Beard, 1984). Sclerophyll shrublands are distributed discontinuously in an arc around the coastal regions of southern and eastern Australia from Kalbarri in Western Australia to Cape York in north-eastern Australia, with outliers of the same community (and sometimes even the same genera) in upland areas of eastern Indonesia. Sclerophyll shrublands always occur on soils highly deficient in available phosphorus and nitrogen (Specht, 1994); the depth of infertile sand to the clayey subsoil varies from several centimetres to greater than 2 m depending on the previous geomorphological history of particular regions.

As with other vegetation types, many subtypes of sclerophyll shrublands can be distinguished on the basis of height (between 0.25 and 2 m) and foliage projective cover (Specht, 1994). The majority occur as patches of varying areal extent close to the present or previous coastline. Sclerophyll shrublands are species-rich communities (especially in south-western Western Australia) with no one taxon dominant; the families Epacridaceae, Myrtaceae, Fabaceae, Restionaceae, Rutaceae and Proteaceae and the genera *Acacia* (Mimosaceae), *Allocasuarina* (Casuarinaceae) and *Xanthorrhoea* (Xanthorrhoeaceae) are common. The structural and floristic features of coastal shrublands (Figs 2, 3, 103) are matched by other shrublands of lesser extent occurring in exposed montane regions and by those above the treeline in alpine environments (Figs 117, 118) (Costin, 1981).

The high floristic diversity of sclerophyll shrublands is matched by diverse responses to different fire frequencies and intensities, as exemplified by a diversity of regeneration mechanisms in the plant community (Gill & Groves, 1981). Another strongly developed feature of such shrublands is their diverse array of nutrient-uptake or nutrient-conservation mechanisms that enable them to grow and survive on nutrient deficient sands (Lamont, 1982).

The second major type of shrubland is that dominated by shrubs of the family Chenopodiaceae — the 'chenopod shrublands' (Leigh, 1994). They occupy about 7 per cent of inland Australia (Fig. 85) on sodium-rich soils with generally a higher clay content in the surface soil than that underlying sclerophyll shrublands. While the latter shrublands are comprised of many genera within a large group of families, the chenopod shrublands are dominated by the genera *Atriplex* and *Maireana* within the one family Chenopodiaceae, as their name implies (Fig. 106). An open-shrubland of sclerophyll species is structurally similar to one dominated by chenopods but the species diversity of the latter is always less and the influence of sodium ions always greater.

Chenopod shrublands are composed of xeromorphic halophytes which are drought- and salt-tolerant (Leigh, 1994). The height of such shrublands may vary from 0.5 m to 3 m (the latter in the case of *Atriplex nummularia)* and with usually low values for foliage projective cover (between 10 and 30%, but sometimes below 10%). Because of this relatively low cover, indigenous and naturalised species of annual and perennial grasses and some forbs typically occur under or between the dominant shrubs. Various admixtures of species of *Atriplex* and *Maireana* occur in different regions mainly in response to different soil types, and in the case of *Maireana*, different species are distributed according to the proximity of the limestone layer to the soil surface (Leigh, 1994).

Grazing of the 'saltbush' (*Atriplex*) country commenced early in the period of European settlement of Australia; while grazing of the dominant shrubs may occur in times of drought, grazing animals prefer to concentrate on the more palatable inter-shrub grasses and forbs. This differential pattern of grazing according to relative palatabilities began a process of degradation of the floristic diversity (and the grazing value) of these chenopod shrublands

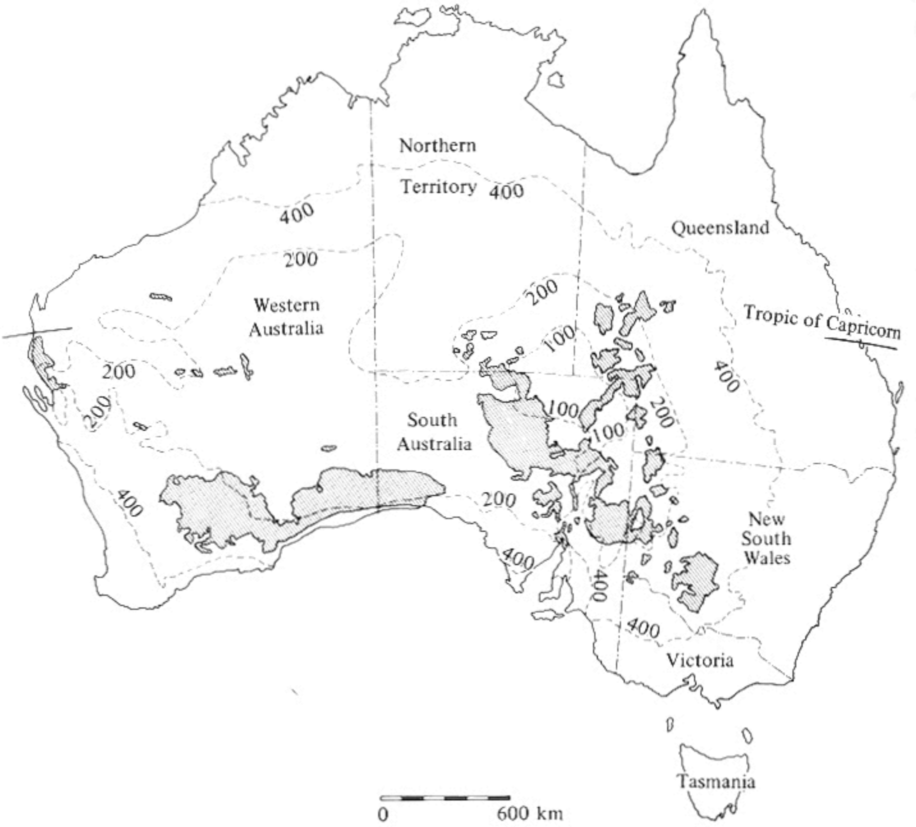

Figure 85. Distribution of chenopod shrublands in relation to the isohyets representing mean annual rainfalls of 100, 200 and 400 mm (dashed lines). Source: J.H.Leigh, Chenopod shrublands, *in* R.H.Groves (ed.), *Australian Vegetation*, 2nd edn, fig. 12.1 (1994). © Cambridge University Press 1981, 1994. Reprinted with the permission of Cambridge University Press and the author.

that has continued. In the worst instances, where the chenopod shrubs are defoliated and/or their stems trampled, only bare areas ('scalds') remain, and these are very difficult to revegetate. In other instances, stable ('disclimax') communities of perennial grasses have replaced the chenopod shrubs and an increase in grazing capacity has resulted, as on the inland riverine plains of New South Wales (Leigh, 1994).

Grasslands

Grasslands are treeless communities dominated by indigenous perennial grasses, usually with some annual grasses and introduced species present (Mott & Groves, 1994).

There are four basic types of grassland in Australia. By far the most widespread are the arid hummock grasslands of central Australia (Fig. 86). These cover as much as a third of the continent in areas with less than 200 mm average annual rainfall which can be either summer- or winter-incident. The arid hummock grasslands are dominated by the genera *Triodia* (Fig. 109) and *Plectrachne* which are referred to as 'hummock' grasses, in that individual clumps are usually large and hemispherical in form.

Areas with a higher rainfall (between 200 and 500 mm/annum) and a predominant pattern of summer rainfall support *Astrebla* species as dominants in what are called arid tussock grasslands (Fig. 108), with *Astrebla* characteristically forming a tussock, i.e. a more or less vertical clump.

The third type is made up of the coastal grasslands of tropical northern Australia. These are dominated by species of *Sporobolus* and *Xerochloa*, and rainfall is again summer-incident.

The fourth type, the subhumid grasslands of eastern Australia, comprises three recognised subtypes. In areas of eastern and northern Queensland with summer rainfall, genera such as *Dichanthium* (Fig. 110) and *Eulalia* form tropical subhumid grasslands, whereas in south-eastern Australia with a predominantly winter or year-round rainfall, temperate grasslands are characterised by tussock grasses belonging to the genera *Themeda*, *Poa* and *Stipa s. lat.* (now mainly included in *Austrostipa*, see Jacobs & Everett, 1996) (Fig. 112). The third subtype, the subalpine tussock grasslands of cold and wet tableland or montane regions of southern Australia (Fig. 111), is dominated by the genera *Poa* and *Danthonia s. lat.* (comprising *Austrodanthonia*, *Notodanthonia* and *Rytidosperma*).

The four basic types of grassland described above represent the natural grassland cover present in different regions of Australia. While some types are extensively distributed, such as the arid hummock grasslands, other grasslands currently exist in south-eastern Australia only as small remnants and were never as widespread as their arid equivalents (Fig. 86).

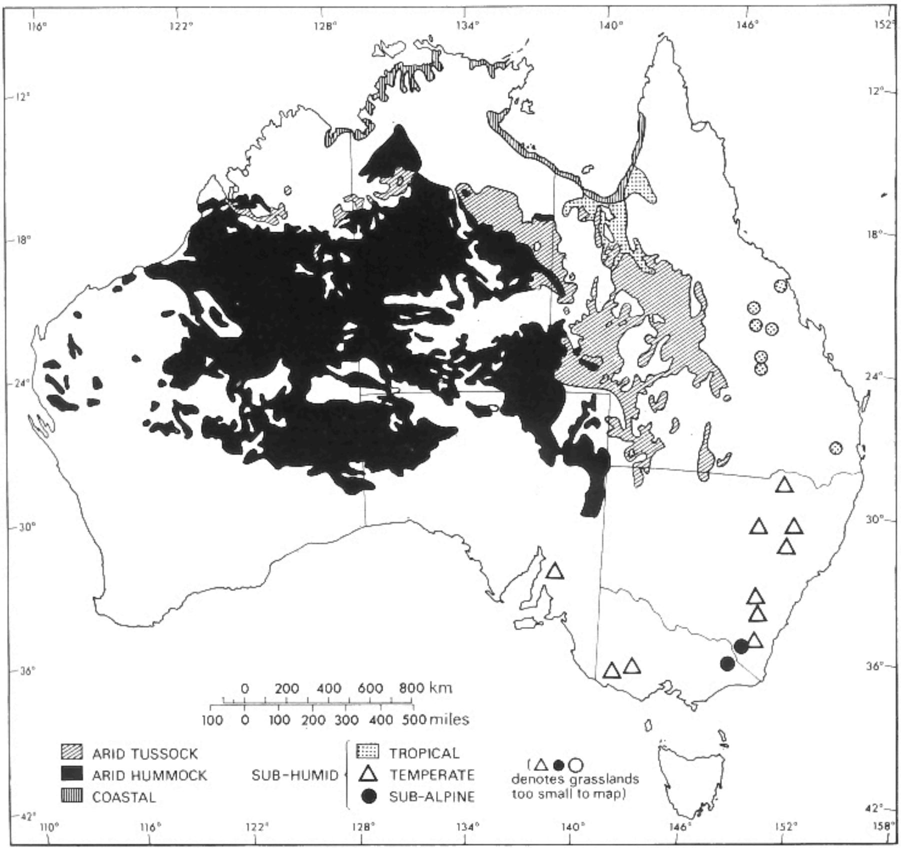

Figure 86. Distribution of major grassland types in Australia. Source: R.H.Groves, fig. 1 (1979). Reproduced with permission.

In addition to these present areas of natural grassland, large areas of derived grasslands now exist in both northern and southern Australia, representing the grassy understorey to the open-woodlands, as described above. Over large areas the overstorey trees have been cleared or thinned and derived or secondary grasslands result. In the north, the grass genera once present in the understorey and now dominant in the derived grasslands include *Themeda* (Fig. 113), *Sorghum* and *Heteropogon*; in south-eastern Australia they are *Themeda, Danthonia s. lat.* and *Poa*, all of which are perennial tussock grasses. In areas of south-eastern Australia with lower rainfall and a history of more intensive sheep grazing, derived grasslands now consist largely of annual grasses and forbs introduced from mediterranean Europe. In such grasslands the indigenous element may be entirely absent.

A range of ecological factors exclude woody vegetation from natural grasslands, even in the absence of grazing. For derived grasslands in relatively humid areas as described above, trees will regenerate naturally provided there is a seed source and protection from grazing and frequent fires. For natural grasslands, inadequate soil moisture seems to be a primary cause of treelessness. While trees will continue to grow adequately from seedlings planted into some treeless areas, they rarely if ever establish naturally. In some instances, as on the Basalt Plains of south-western Victoria, tree seedlings seem unable to establish because the clay soil on which most grasslands occur cracks deeply on drying and there is inadequate moisture for early root growth. Below an average annual rainfall of about 250 mm, as in at least a third of Australia, both establishment *and* growth of trees are prevented. Only in the localised cases of inverted treelines ('frost hollows') in subalpine regions does soil moisture seem not to be implicated. In these situations a short exposure to winter temperatures lower than usual may kill even established seedlings of *Eucalyptus pauciflora.*

If soil moisture limits tree seedling establishment in natural grasslands, the interaction between grazing and fire seems especially important in maintaining the herbaceous character of derived grasslands. If grazing occurs soon after a fire and continues, then the regenerative capacities of some grasses are so severely depleted that botanical composition of the grassland changes. In southern Australia this change usually favours the grass genera having a C3 photosynthetic pathway such as *Danthonia s. lat.* and *Stipa*, at the expense of the C4 *Themeda* element. But the same interaction seems to influence the balance between *Heteropogon* and *Themeda* (both C4 grasses) in grazed and regularly burnt grasslands in tropical Queensland. In the arid hummock grasslands of north-western Western Australia, burning and deferred grazing restricts the growth of *Triodia pungens,* a relatively undesirable species for animal production, and promotes the growth of other, more desirable *Triodia* species (Suijdendorp, 1981). The proportions of the dominant species in both types of grasslands may also change in relation to other ecological factors, of which soil nutrient status and temperature are the main ones (see Moore, 1970, and Groves & Williams, 1981, for further examples).

Floristic classification of Australian vegetation

The classificatory basis for Australian vegetation of Specht (1970), Beard (1976), Carnahan (1976, 1977, 1990) and many others is structural, and this approach has a considerable following. However, another approach to describing vegetation is floristic, a recent example being that of Bridgewater (1994).

Bridgewater (1994) recognised and mapped 26 Divisions, and a further 11 Divisions were defined on an ecological basis without being mapped. Each Division was defined by a suite of 'character genera'. The geographically-defined Divisions are shown in Fig. 87. Characteristics of the Divisions are shown in Table 26 (note that some of the 'genera' are in fact subgenera or 'Alliances' of *Eucalyptus* and these are shown in quotation marks in Table 26).

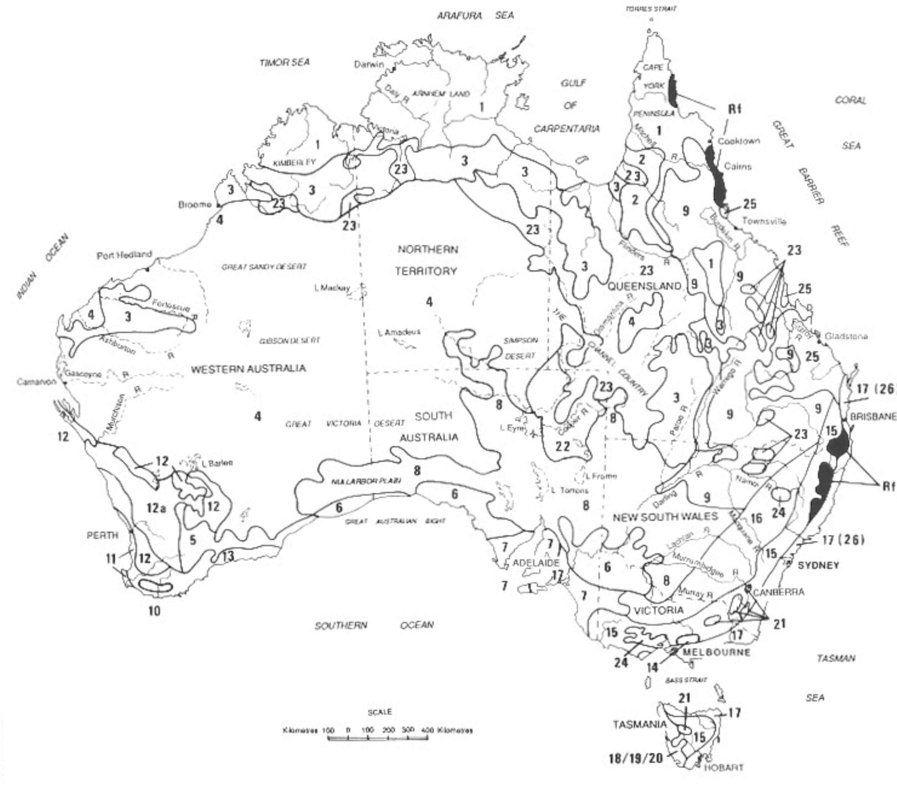

Figure 87. Floristic vegetation Divisions for Australia. The numbers refer to the Divisions as described in Table 26. Rf = areas where rainforest patches dominate the landscape. Reproduced with permission.

Table 26. The floristic divisions, character genera, structure and distribution of the Australian flora (after Bridgewater, 1994).

Division	Character genera	Structure & distribution
1. Blakella-Gardenia Division	'*Blakella*', *Corymbia*, '*Symphyomyrtus*', '*Eudesmia*', *Livistona*, *Adansonia*, *Gardenia*, *Erythrophleum*, *Terminalia*, *Buchanania*, *Xanthostemon*, *Grevillea*, *Callitris*, *Themeda*, *Aristida*, *Eriachne*, *Heteropogon*, *Mnesithea*, *Cymbopogon*, *Sorghum*	Forest to open woodland in tropical northern Australia. Often *Eucalyptus* species and genera of the Indo-Malayan monsoonal forest with a tall grass understorey
2. Melaleuca-Sorghum Division	*Melaleuca*, *Sorghum*, *Chrysopogon*, *Heteropogon*, *Pandanus*, *Terminalia*, *Bauhinia*, *Xerochloa*, *Alphitonia*, *Barringtonia*	Open savannah around the Gulf of Carpentaria, dominated by *Melaleuca* with a tall grass understorey; inundated in wet season
3. Acacia-Triodia Division	*Acacia*, *Corymbia*, '*Symphyomyrtus*', *Owenia*, *Calytrix*, *Erythrophleum*, *Grevillea*, *Solanum*, *Verticordia*, *Jacksonia*, *Terminalia*, *Pityrodia*, *Callitris*, *Triodia*, *Plectrachne*, *Eriachne*	Open woodland with stunted *Eucalyptus* and *Acacia* species, a (hummock) grass understorey and occasional low shrubs
4. Duboisia-Triodia Division	*Duboisia*, '*Eudesmia*', '*Symphyomyrtus*', *Allocasuarina*, *Santalum*, *Codonocarpus*, *Tribulus*, *Zygophyllum*, *Hakea*, *Grevillea*, *Dodonaea*, *Eremophila*, *Senna*, *Abutilon*, *Triodia*, *Aristida*, *Plectrachne*	Hummock grasslands of central and central-western Australia with tree shrub cover of variable density
5. Eudesmia-Banksia Division	'*Eudesmia*' '*Symphyomyrtus*', *Banksia*, *Chamaelaucium*, *Chorizema*, *Lambertia*, *Leucopogon*, *Lysinema*, *Xanthorrhoea*, *Petrophile*, *Allocasuarina*, *Jacksonia*, *Dryandra*, *Templetonia*, *Verticordia*, *Stirlingia*, *Kennedia*, *Loxocarya*, *Mesomelaena*, *Anarthria*, *Stylidium*	The western mallee, with an understorey of sclerophyllous shrubs
6. Symphyomyrtus-Sclerolaena Division	'*Symphyomyrtus*', *Sclerolaena*, *Maireana*, *Senna*, *Eremophila*, *Myoporum*, *Santalum*, *Melaleuca*, *Zygophyllum*, *Dodonaea*, *Calytrix*, *Lycium*, *Triodia*	Mallee, on solonised soils, with many halophytic shrubs in the understorey
7. Symphyomyrtus-Danthonia Division	'*Symphyomyrtus*', *Leptospermum*, *Grevillea*, *Thysanotus*, *Pultenaea*, *Lasiopetalum*, *Dampiera*, *Astroloma*, *Acrotriche*, *Baeckea*, *Goodenia*, *Melaleuca*, *Danthonia s. lat.*, *Austrostipa*	The eastern mallee, with a mixed shrub and grass understorey

Table 26 continued

Division	Character genera	Structure & distribution
8. Maireana-Sclerolaena Division	*Acacia, Maireana, Sclerolaena, Chenopodium, Halosarcia, Nitraria, Lycium*	Low shrublands of eastern and central-southern Australia, dominated by Chenopodiaceae, with occasional *Acacia*; soils often saline or alkaline
9. Geijera-Paspalidium Division	*Geijera, Flindersia, Carissa, Eremophila, Eremocitrus, Capparis, Sclerolaena, Enchylaena, Sida, Terminalia, Acacia, Atalaya, Heterodendron, Chloris, Paspalidium, Sporobolus, Aristida, Cymbopogon, Eragrostis*	Open woodland with a dense grass understorey, and including a number of monsoon forest genera in the tree layer. Now heavily impacted by grazing. Northern Queensland to northern New South Wales, west of the Great Dividing Range
10. Allocasuarina-Trymalium Division	'*Symphyomyrtus*', *Allocasuarina, Paraserianthes, Trymalium, Thomasia, Mirbelia, Phebalium, Banksia, Chorilaena, Burtonia, Chorizema, Crowea, Veronica, Stylidium, Leucopogon, Agonis, Clematis, Bossiaea, Hovea, Tremandra, Persoonia, Podocarpus*	Wet sclerophyll, well stratified forest of south-western Australia (Karri or Tingle forest). Fire normally absent, and trees regenerating from seed rather than coppicing if burnt
11. Acacia-Leucopogon Division	'*Symphyomyrtus*', '*Monocalyptus*', '*Eudesmia*', *Acacia, Leucopogon, Dryandra, Pimelea, Hakea, Jacksonia, Hibbertia, Conospermum, Melaleuca, Phyllanthus, Xanthorrhoea, Scaevola, Templetonia, Spyridium, Calothamnus, Diplolaena, Myoporum, Olearia, Lomandra, Lepidosperma, Conostylis, Mesomelaena, Austrostipa*	A complex of low shrubland with some tall forest, on recent calcareous sands in a narrow coastal zone of south-western Australia
12. Banksia-Nuytsia Division	'*Monocalyptus*', *Corymbia*, '*Symphyomyrtus*', *Acacia, Banksia, Nuytsia, Actinostrobus, Xylomelum, Hybanthus, Gompholobium, Burchardia, Stirlingia, Persoonia, Melaleuca, Conospermum, Verticordia, Hypocalymma, Allocasuarina, Hibbertia, Leucopogon, Eremaea, Dryandra, Hakea, Grevillea, Jacksonia, Lechenaultia, Stylidium, Anigozanthos*, etc	A complex of forests and shrublands, generally on sands and laterites, in south-western Australia

Table 26 continued

Division	Character genera	Structure & distribution
13. Agonis-Persoonia Division	*Corymbia*, '*Monocalyptus*', *Allocasuarina*, *Agonis*, *Adenanthos*, *Banksia*, *Hakea*, *Leucopogon*, *Persoonia*, *Regelia*, *Synaphea*, *Verticordia*, *Oxylobium*, *Burtonia*, *Gompholobium*, *Styphelia*, *Hypocalymma*, *Boronia*, *Melaleuca*, *Petrophile*, *Isopogon*, *Grevillea*, *Lechenaultia*, *Patersonia*, *Xanthorrhoea*, *Kingia*, *Dasypogon*, *Anarthria*, *Loxocarya*, *Macrozamia*	An extremely species-rich complex of forest, shrubland and coastal communities on nutrient-poor soils
14. Bedfordia-Pomaderris Division	'*Symphyomyrtus*', *Bedfordia*, *Pomaderris*, *Coprosma*, *Lomatia*, *Olearia*, *Atherosperma*, *Hedycarya*, *Clematis*, *Dicksonia*, *Australina*, *Lepidosperma*, *Gahnia*, *Tetrarrhena*, *Cyathea*, *Microsorium*	Well stratified wet sclerophyll forest dominated by very tall *Eucalyptus* (especially *E. regnans*) with a tree understorey of Monimiaceae and Asteraceae. Dominant taxa fire-susceptible and regenerating from seed, not coppicing
15. Cassinia-Daviesia Division	'*Symphyomyrtus*', '*Monocalyptus*', *Cassinia*, *Daviesia*, *Leucopogon*, *Viola*, *Coprosma*, *Tetratheca*, *Prostanthera*, *Epacris*, *Xanthorrhoea*, *Astroloma*, *Lissanthe*, *Pimelea*, *Platylobium*, *Banksia*, *Platysace*, *Dillwynia*, *Stylidium*, *Persoonia*, *Correa*, *Hibbertia*, *Caustis*, *Dichelachne*, *Danthonia s. lat.*, *Themeda*, *Austrostipa*, *Lomandra*, *Lepidosperma*, *Microlaena*, *Dianella*, *Hypolaena*, *Cladium*	The 'damp sclerophyll' forests of south-eastern Australia, largely on, but not confined to, the Great Dividing Range
16. Astroloma-Bursaria Division	'*Symphyomyrtus*', '*Monocalyptus*', *Astroloma*, *Acrotriche*, *Lissanthe*, *Callitris*, *Bursaria*, *Dichelachne*, *Lomandra*, *Hydrocotyle*, *Dichondra*, *Brachychiton*, *Gonocarpus*, *Indigofera*, *Wahlenbergia*, *Dodonaea*, *Poa*, *Themeda*, *Echinopogon*, *Austrostipa*	Forest on the drier western slopes of the southern Great Dividing Range, with a range of understoreys. Now much disturbed by Aboriginal and European burning practices and agricultural use
17. Banksia-Leptospermum Division	'*Monocalyptus*', *Corymbia*, *Angophora*, *Banksia*, *Leptospermum*, *Telopea*, *Epacris*, *Monotoca*, *Persoonia*, *Dillwynia*, *Dampiera*, *Melaleuca*, *Sprengelia*, *Lambertia*, *Darwinia*, *Baeckea*, *Westringia*, *Lasiopetalum*, *Allocasuarina*, *Pultenaea*, *Hakea*, *Xanthorrhoea*, *Kunzea*, *Xylomelum*, *Patersonia*, *Doryanthes*, *Lepidosperma*, *Leptocarpus*, *Tetrarrhena*, *Hypolaena*, *Caustis*	A complex of forests and shrublands on a range of soils, from dry sandstone to permanently wet peats, in diverse habitats, from the Mt Lofty Range and Kangaroo Island in the west to the vicinity of Brisbane in the east, and south to Tasmania

Table 26 continued

Division	Character genera	Structure & distribution
18. Nothofagus Division	*Nothofagus, Atherosperma, Anodopetalum, Polystichum, Eucryphia, Prionotes, Cenarrhenes, Tasmannia, Phyllocladus, Dacrydium, Doryphora, Elaeocarpus, Ceratopetalum, Cyathea, Dawsonia, Blechnum, Microsorium, Grammitis, Dicksonia, Tmesipteris*	Rainforest pockets from Tasmania to Queensland
19. Athrotaxis-Tasmannia Division	*Athrotaxis, Agastachys, Orites, Tasmannia, Cyathodes, Richea, Monotoca, Astelia, Trochocarpa, Podocarpus, Nothofagus, Oreomyrrhis, Epacris, Hydrocotyle*	Low forest and shrubland of the high country of central and western Tasmania
20. Gymnoschoenus Division	*Gymnoschoenus, Sprengelia, Schoenus, Xyris, Tetrarrhena, Epacris, Gleichenia, Comesperma, Lepidosperma, Empodisma, Sphagnum*	Tall tussock sedgeland on peaty plains of western Tasmania
21. Poa-Ranunculus Division	*Poa, Ranunculus, Danthonia s. lat., Viola, Plantago, Luzula, Acaena, Asperula, Epacris, Oreobolus, Celmisia, Craspedia, Pentachondra, Leucopogon, Baeckea, Pultenaea, Wahlenbergia, Wittsteinia, Gaultheria, Restio, Astelia, Empodisma, Carex, Deyeuxia, Sphagnum*	Shrublands and grasslands in alpine regions of south-eastern Australia
22. Zygochloa-Acacia Division	*Acacia, Atriplex, Psoralea, Solanum, Sclerolaena, Zygochloa, Aristida, Eragrostis*	The true 'desert' communities dominated by canegrass (*Zygochloa*), on red sands in very low rainfall areas
23. Astrebla-Dichanthium Division	*Hibiscus, Sida, Psoralea, Crotalaria, Chenopodium, Atriplex, Astrebla, Dichanthium, Bothriochloa, Eulalia, Cymbopogon, Aristida, Eriachne, Eragrostis*	Grasslands of northern Australia. Subject to heavy grazing pressure in many areas, and threatened in places by the introduced *Acacia nilotica*
24. Themeda-Stipa Division	*Themeda, Austrostipa, Danthonia s. lat., Eryngium, Leptorhynchos, Plantago, Schoenus, Helichrysum s. lat., Tricoryne, Geranium*, Orchidaceae	Now mainly reduced to remnant patches, often invaded with introduced genera
25. Angophora-Syncarpia Division	*Corymbia*, '*Symphyomyrtus*', '*Monocalyptus*', '*Idiogenes*', *Angophora, Elaeocarpus, Tristaniopsis, Cupaniopsis, Backhousia, Archontophoenix, Syncarpia, Ceratopetalum, Toona, Dendrocnide, Trema, Ficus, Rhodomyrtus, Wickstroemia, Culcita, Doodia, Cyathea, Blechnum, Themeda, Imperata*	Coastal forest, with some inland extensions, in Queensland north of the Tropic of Capricorn

Table 26 continued

Division	Character genera	Structure & distribution
26. Syncarpia-Ceratopetalum Division	*Syncarpia, Ceratopetalum, Angophora,* '*Symphyomyrtus*', *Corymbia,* '*Monocalyptus*', *Lophostemon, Backhousia, Acmena, Doryphora, Livistona, Notolaea, Rapanea, Callicoma, Phebalium, Doodia, Culcita, Todea, Gahnia*	Dense forest with a fern-rich understorey, on the eastern slopes of the Great Dividing Range, and intermixed with Division 17
27. Allosyncarpia Division	*Calophyllum, Carpentaria, Pouteria, Syzygium, Podocarpus, Xanthostemon, Alstonia, Flagellaria, Fimbristylis*	Patchy, perhaps relictual, in Arnhem Land of the Northern Territory
28. Muehlenbeckia Division	*Muehlenbeckia, Echinochloa, Eragrostis, Chenopodium, Trigonella, Cyperus, Scirpus, Carex*	Found in flood channels of river beds of the 'Channel Country' of Queensland and South Australia
29. Spinifex-Cakile Division	*Spinifex, Tetragonia, Zoysia, Distichlis, Cakile, Arctotheca*	Sand dune community of the southern coasts
30. Canavalia-Ipomoea Division	*Canavalia, Ipomoea, Boerhavia, Spinifex*	Sand dune community of the tropics
31. Baumea Division	*Baumea, Cladium, Schoenoplectus*	Emergent vegetation in freshwater wetlands of southern Australia
32. Baumea-Leptocarpus Division	*Baumea, Leptocarpus, Gahnia, Lepidosperma, Restio, Chorizandra*	A range of associations, found in fresh or brackish swamps in southern Australia
33. Phragmites Division	*Phragmites, Typha, Scleria*	Vegetation of freshwater swamps or lagoons in tropical or temperate areas, where there is flowing water
34. Typha Division	*Typha, Azolla, Spirodela, Eleocharis*	Vegetation of standing or flowing eutrophic waters in coastal and inland areas
35. Hymenachne-Oryza Division	*Hymenachne, Oryza, Eleocharis, Cyperus, Leersia, Pseudoraphis, Panicum, Nymphaea, Polygonum, Nelumbo*	Vegetation of lagoons and flood plains in the coastal tropics. Can be inundated for 3–4 months of the year
36. Heterozostera-Amphibolus Division	*Heterozostera, Amphibolis, Posidonia*	Seagrass beds of shallow estuaries of southern and south-western areas
37. Halophila-Cymodocea Division	*Halophila, Cymodocea, Thalassia, Thalassodendron*	Seagrass vegetation north of the Tropic of Capricorn. Overlaps with Division 36 near Shark Bay, Western Australia

Patterns at regional scales

The structural description of present vegetation in Australia given earlier omits some specialised vegetation types, such as those in which either saline or fresh water, coastal salt-laden winds or low temperatures play a major role (but see Adam, 1994; Brock, 1994; Clarke, 1994; and Williams & Costin, 1994, respectively for details of the vegetation of these extreme habitats, and the chapter on aquatic vegetation in this volume). The five major structural vegetation types described above have been categorised on the basis of plant height and foliage projective cover. Some aspects of floristic variation and the ecological factors controlling such variation within these categories have been mentioned briefly. Vegetation rarely falls into neat categories, however; instead, it usually varies along a continuum or gradient in which many factors interact in a highly complex way. The following section describes the regional patterning of vegetation types along transects in several different parts of Australia, in order to present something of the ecological complexity and the dynamic nature of present Australian vegetation. Many other examples could have been given, but consideration of these is beyond the scope and capacity of this volume. For more details see Groves (1994).

Aridity gradient

A transect from the coastline towards the centre of the continent is characterised by an increase in aridity. The concentric pattern of decrease in total annual rainfall, from as much as 3500 mm to as little as 125 mm, irrespective of its seasonal incidence (Fig. 88), broadly matches the concentric distribution of the major vegetation types shown in Fig. 82. Closed-forests typical of high rainfall areas close to the eastern coast (1000–2500 mm) merge into tall open-forests of the coastal mountains which in turn grade into low open-forests or tall woodlands typical of drier, inland areas (sometimes occurring as tablelands), and especially if they are the inland 'slopes' of the coastal mountain chain. Further inland still, low woodlands of mallee eucalypts (in the south) or of acacias (in the north) may be intermixed with chenopod shrublands in regions having an annual rainfall of between 500 and 250 mm. In the arid centre, these vegetation types may persist in special ecological situations, but generally hummock grasslands dominated by *Triodia* species, of yet lower stature, become more common in regions having an annual rainfall below about 200 mm. Physiographic complexity, especially in the arid zone (Mabbutt, 1969), together with the distribution of soil types, may singly or together modify this general pattern of vegetation induced by aridity. Only in two regions – that abutting the Nullabor Plain in South and Western Australia, and the central west coast of Western Australia – do arid communities occur at the coastline proper.

The gradient in aridity from coast to inland is accompanied by a gradient in rainfall variability, in which coastal rainfall is generally much less variable on average than that in the inland. This variability increases with increasing aridity and the vegetation shows adaptations to such variability, especially by the 'desert ephemeral' element in the arid zone vegetation complex. For example, for the annual flora of the arid Murchison region of Western Australia (less than 200 mm annual rainfall, which can occur at any time of the year), winter rainfall leads to a predominantly dicotyledonous flora, whereas the flora germinating after summer rains is largely made up of monocotyledons, especially grasses (Mott, 1972). This difference could be related to the different temperatures required for seed germination – the summer flora requiring a higher temperature for germination than the winter flora (Mott, 1972). The further along the gradient in aridity then the more likely it seems to be that the vegetation is adapted to irregular episodic events, rather than to the 'average' rainfall amounts as shown in Fig. 88.

At the moist end of the gradient, the land on which closed-forests and tall open-forests grow is an important source of potable water for Australian cities as well as for hardwood timber of high quality. On the east coast much of the land formerly covered by closed-forest has been cleared for crops such as sugar (in the north) or for dairy pasture. The low open-forests and woodlands further inland have mostly been greatly modified and are now used for

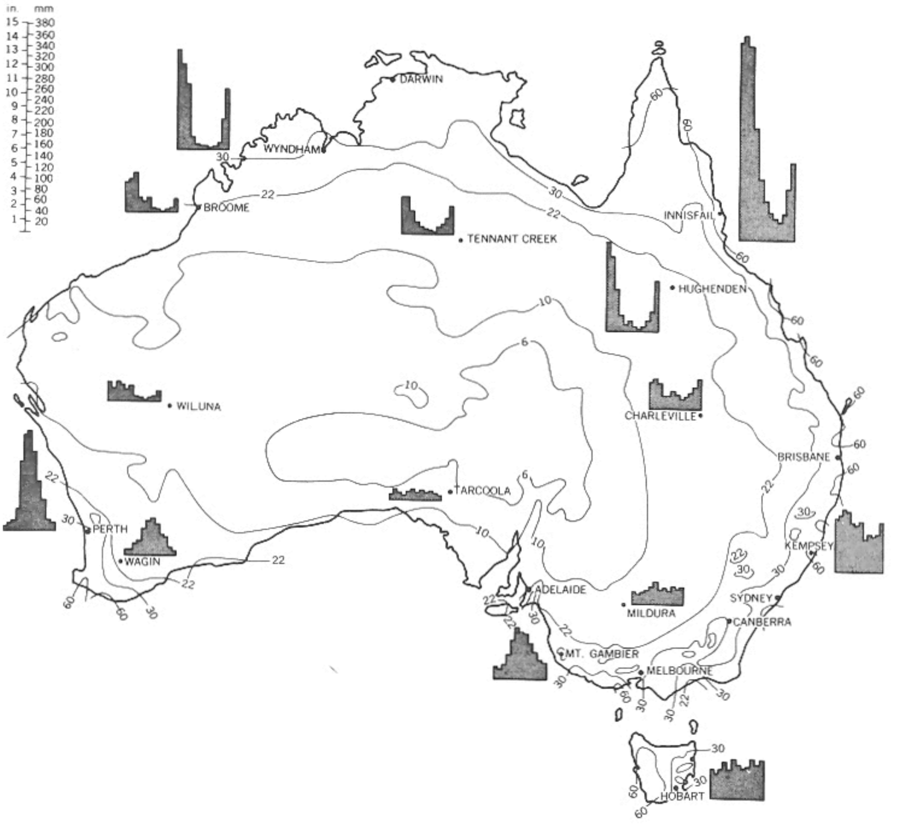

Figure 88. Mean monthly rainfall of selected recording stations with the mean annual rainfall (in./mm) being recorded under each diagram. Source: adapted from Climate and Meteorology of Australia, Bulletin no. 1 (reprint from official Year Book of Commonwealth of Australia, 1965). Reproduced with permission.

grazing and/or cropping. Chenopod shrublands are extensively grazed by sheep, while the mosaic of more arid vegetation types in central Australia is grazed by cattle or sheep as well as by feral animals. All the vegetation types have value for nature conservation although the grassy woodlands and grasslands are least well represented in the total system of conservation reserves.

Nutrient gradient

Australian soils are in general poor in nutrients, especially nitrogen and phosphorus, and much of the native flora has evolved in this regime. In fact, additional nitrogen and phosphorus, at the levels usually employed in agriculture and horticulture, can be toxic to many native plants. As a consequence of the depauperate nutrient levels of natural soils, few examples of major nutrient gradients affecting vegetation patterns can be found. The following is one case study.

The Sydney Basin region on the central east coast of the continent comprises three main Series of Triassic rocks. Wianamatta shales overlie sandstones of the Hawkesbury Series which in turn overlie Narrabeen shales and sandstones. Below all three types of parent rock lie Permian coal-containing sandstones. Uplift of these strata subsequent to their deposition has led to complex physiographic patterning of the landscape in areas such as the Blue Mountains west of Sydney. Furthermore, remnants of Tertiary basalt flows are found on some areas of the uplifted tablelands, as at Mount Wilson. Such complex geologic and physiographic patterning is matched by an equally complex mosaic of vegetation types.

Results of ecological studies in the Sydney region date back almost 100 years to Cambage (1907) and Andrews (1916); collectively, the results show that the different vegetation types in the region are distributed predominantly along a soil nutrient gradient – specifically soil phosphorus and/or nitrogen gradients – which in turn reflect the phosphate status of the parent rock type (see e.g. Beadle, 1954, 1962; Hannon, 1958). Typically, low woodlands and sclerophyll shrublands occur on the Hawkesbury sandstones which are lowest in soil phosphorus. Low open-forest occurs on lateritic soils with somewhat higher soil phosphorus levels, while tall open-forests and small areas of closed-forest ('rainforest') are confined to soils higher in phosphorus derived from Narrabeen shales and sandstones. The closed-forests occur on those soils highest in phosphorus, and especially when they are derived from Tertiary basalts (see Beadle, 1962, for typical soil phosphorus levels).

More recent findings of Burrough *et al.* (1977) show that factors other than soil nutrients may also be significant in accounting for the mosaic of vegetation types in the Sydney region. They showed that the patterning of open-forest, woodland, sclerophyll shrubland and sedgeland – which all occur on Hawkesbury sandstone – could be explained primarily by soil moisture differences, expressed either as mean annual rainfall or as different levels of impedance of soil drainage (in the case of shrublands and sedgelands).

The complex distribution pattern of a range of present vegetation types of the Sydney region thus may be partly accounted for by differences in soil nutrient levels. From the findings of Burrough *et al.* (1977), however, it becomes clear that the same vegetation types may be distributed along gradients of other factors such as soil moisture. Whether the soil nutrient gradient is primary remains to be clarified for this and other regions. The physiographic complexity of the Sydney Basin will probably always complicate any simple explanations based on single ecological factors and their influence on the distribution of present vegetation types.

Fire

The role of fire frequency in distinguishing closed- from open-forests has already been referred to above. In summary, in high rainfall areas of Tasmania and southern Victoria, a fire occurring more frequently than once in about every 400 years will prevent the dominance of the closed-forest species *Nothofagus cunninghamii* and maintain dominance of eucalypts, such as *Eucalyptus regnans.* A fire frequency of between about 80 and 400 years will be associated with an overstorey of characteristic tall open-forest eucalypts with some closed-forest floristic elements in the understorey. At fire frequencies less than 80 years *Acacia* species, such as *A. melanoxylon*, will be prominent; at frequencies less than about 20 years, treeless shrub- and sedge-grasslands will be perpetuated (Jackson, 1968; Ashton 1981). Thus variation in fire frequency may play a major role in determining vegetation patterning in this region of south-eastern Australia.

A fire regime is composed not just of fire frequency, however, but also of fire intensity and season of fire (Gill, 1975). Differences in the latter two components may also influence the distribution of present vegetation types. Around the area of Darwin in the Northern Territory, a native grass *Sorghum intrans* occurs as a dominant understorey species in eucalypt woodland. In many areas, this grass has now been replaced by the introduced species *Andropogon gayanus* (Gamba grass) and *Pennisetum polystachion* (Mission grass), which together produce fuel loads three to four times that of the native species which they have replaced (Anderson, 1997). Furthermore, the introduced grasses dry out later in the season when fire danger may be higher. When fire occurs, it is of a higher intensity and later in the season than if the native grass still dominated the understorey. Two components of the fire regime are thus changed as a result of the invasion by introduced grasses, with a consequent increase in fire hazard and a reduced value of the vegetation for nature conservation.

The influence of fire on Australian vegetation types operates at the level of individual taxa, and some Australian plant genera show specific adaptive responses to fire regimes. For instance, some geophytes (including several orchids) and the genera *Xanthorrhoea* and *Kingia* are usually stimulated to flower or flower more heavily after a fire, although their need for fire might not be obligate. Some species of *Banksia*, *Casuarina/Allocasuarina* and *Eucalyptus* may be stimulated to release seed from their woody aerial fruits in response to heat and/or desiccation The seeds thus land on an ash-bed that is more favourable in terms of nutrient levels and absence of competitors than a pre-fire microsite. For other genera, such as *Acacia* and many other leguminous shrubs, which store their seed not aerially but in the soil, fire may stimulate germination of those soil-stored seeds. The extent of germination will depend mainly on fire intensity and how deeply the heat from the fire may penetrate the soil profile. After a fire, light intensity will be higher and this increase together with endogenous hormonal changes may result in bud development being stimulated. This response is shown by many genera which have epicormic buds buried in their stem tissue or have aggregations of such buds at their base as lignotubers. This latter response is shown by the 'sprouters' in the Australian flora, of which many species in the genera *Eucalyptus* (Fig. 99), *Hakea*, *Grevillea* and *Banksia* are good examples.

Gill (1981) has classified these responses into seven different categories (Table 27). Gill's scheme separates firstly the plants killed by fire (non-sprouting) from those that recover from the effects of fire by sprouting. Such a primary difference is not diagnostic of different genera, however, and species within the same genus can respond differently. Some genera (e.g. *Hakea*, see Barker *et al.*, in press) can contain species exhibiting almost all sprouting/non-sprouting types. Most communities of Australian plants show a mixture of these different adaptive responses.

Table 27. A simple classification of adaptive responses to fire in vascular plants (table 2 of Gill, 1981).

Reproductive Strategy	Response Type
A. Plants in the reproductive phase just subject to 100% leaf scorch by fire die (non-sprouters)	
(a) Seed storage on plant	I
(b) Seed storage in soil	II
(c) No seed storage in burnt area	III
B. Plants in the reproductive phase just subject to 100% leaf scorch by fire recover (sprouters)	
(a) Subterranean regenerative buds	
(i) Root suckers, horizontal rhizomes	IV
(ii) Basal stem sprouts, vertical rhizomes	V
(b) Aerial regenerative buds	
(i) Epicormic buds grow out	VI
(ii) Continued outgrowth of active aerial prefire buds	VII

While the general responses of many Australian plant genera and species to fire have been described, it is important to recognise that particular fire regimes are but one of the many environmental stresses on Australian plants. Other stresses may include water deficit or excess, extreme cold, herbivore attack, and their interactions.

Fire has been a major ecological factor influencing Australian vegetation types for a long time, at least since the Tertiary period (Kemp, 1981). The different species or species groups comprising those vegetation types have evolved a range of adaptations to its incidence (Gill, 1975). Because of variation in intensities and frequencies, as well as in seasonal occurrence, fire regimes are often unique and few generalisations may be tenable on which to base future management of present Australian vegetation types. The gap between existing knowledge of fire effects and the widespread implementation of management practices, such as prescribed burning, remains considerable, although it is gradually closing.

Grazing

Grazing by domesticated stock over a period as long as 200 years has induced floristic changes in many Australian vegetation types, but none more so than in the woodlands and grasslands of south-eastern Australia. A general change from perennial grass cover to a shallower-rooted annual one has already been noted above. One such sequence of species changes that is well documented has occurred in *Eucalyptus melliodora/E. blakelyi* woodlands on the Southern Tablelands of New South Wales (Table 25). Moore (1970) considered that this sequence was also representative of the changes resulting from grazing other woodlands dominated by *E. camaldulensis* and *E. leucoxylon* in both western Victoria and South Australia.

The discovery of routes across the Great Dividing Range from 1812 onwards enabled grazing of the inland temperate woodlands by sheep and cattle to commence. As grazing intensified the tall warm-season perennial tussock grasses (mainly *Themeda triandra* and *Stipa aristiglumis*) that originally dominated the understorey to these woodlands were replaced by predominantly shorter cool-season grass species of *Danthonia s. lat.* and *Stipa s. lat.* This change was in turn followed by an increasing dominance of cool-season annual legumes and other herbs, usually of Mediterranean origin. Because this stage of the sequence was usually of higher nutritional quality, especially through winter, it was subsequently maintained and even promoted by regular applications of superphosphate fertilizer, which in turn led to dominance of the introduced annual legume *Trifolium subterraneum* and elimination of *Danthonia s. lat.* and other native perennials. Although there are regional variations, especially according to the relative incidence of summer- and winter-rainfall, this general pattern applies over much of south-eastern Australia.

Recognition of the acidifying effect of repeated superphosphate application, together with increases in fertilizer cost, have subsequently led to reductions in the levels of fertilizer applied to these areas of former woodland. This has been accompanied by a reversion of some grazed grasslands back to those dominated once again by native cool-season perennial grasses, such as species of *Danthonia s. lat.* Novel and more sustainable systems of grazing management are now having to be developed to accommodate these recent floristic changes.

Almost 200 years of grazing by sheep and cattle have been accompanied by significant floristic changes to the understoreys of eucalypt woodlands in south-eastern and south-western Australia. So complete have these changes been in most areas that representative samples remain of the original understorey only in a few cemeteries and some travelling stock routes and roadsides. On all grazed areas, the trees are over-mature and few in number. Thus the conservation status of these long-grazed woodlands and grasslands is now precarious and increasingly uncertain in the future.

Salt gradient

In south-western Western Australia, a transect inland from the west coast close to Perth moves in general from sclerophyll shrubland or low open-forest dominated by *Banksia* on the Swan coastal plain to open-forests of low or medium height dominated by various species of

Eucalyptus along the Darling Escarpment. This change in vegetation type corresponds with an increase in annual rainfall and a change in substrate from deep sand to a lateritic podzol, both soil types being relatively low in available nutrients. Further eastwards eucalypt woodlands predominate, with the mallee habit becoming more prominent as rainfall decreases with increasing distance from the west coast. Further eastwards still, chenopod shrublands may occur intermixed with eucalypt woodland.

Clearance of the deep-rooted eucalypt woodlands on the eastern face of the Darling Range and the growing of either cereals or equally shallow-rooted annual pasture species have led over time to an increasing local problem of salting of both agricultural land and surface water in the region. Saunders & Hobbs (1992) cited data for this region which showed that nearly 3 per cent of cleared land was already affected by salinity and that this level could increase to more than 15 per cent in the next 30 years. Such increased salinity in this inland region has serious implications for the ever-increasing need for either surface- or ground-water of potable quality for the city of Perth, the inland salted region being the 'catchment' for much of the surface-water on which Perth depends. Only retention of the remaining natural vegetation and strategic replanting with deep-rooted tree species in this catchment area can ameliorate the increasing salinization of Perth's drinking water. In this instance it is the gradual change over about 150 years from perennial, deep-rooted native vegetation to annual, shallow-rooted herbaceous crops and pastures which has induced the long-term change in salinity levels. Whether reversion to something resembling the original vegetative state will halt the further degradation in water quality is for the future to discover.

The consequences of the change from native perennial vegetative cover to introduced annual vegetation described above applies even more so to the entire south-eastern Australian region, where it has been exacerbated by the development of irrigation schemes along the Murray and Darling Rivers. In this large region the effects of clearance of native vegetation have taken longer to express themselves, but a similar ecological scenario is developing, with equally dire consequences for continued agricultural land use and the provision of potable water for large cities such as Adelaide.

Introduced plants

About 15 per cent of the total Australian vascular flora has been introduced from outside Australia, with the proportion varying according to the degree of disturbance of the natural vegetation. The proportion is highest on islands such as Norfolk (viz. 60%) and lowest in the Northern Territory and in the Kimberley region of Western Australia (about 5%) (see table 2.1 of Humphries *et al.,* 1991). For the last 100 years, it seems that the average rate of naturalisation of these introduced plant species has been about six species per year in each of the southern States (Specht, 1981). Many of these species have seemingly little effect on the natural vegetation, while a significant minority of the total are major weeds in that they affect human well-being in some deleterious way. Such weeds may reduce production of crops or pastures, either directly or indirectly. Other introduced plants may affect human health in diverse ways. Yet other introduced plants – those known collectively as 'environmental weeds' – may reduce native plant or animal biodiversity and thereby affect the functioning and conservation of natural vegetation.

The vegetation types most affected by introduced plants are probably the coastal vegetation, temperate grasslands and woodlands of south-eastern Australia. For instance, the ground stratum of much of Australia's eucalypt woodlands has in many cases been either completely or substantially replaced by introduced plants, with drastic consequences for the conservation of some native animal groups such as insects and reptiles. In instances where the introduced plants are legumes able to fix atmospheric nitrogen, soil nitrate levels will be raised, ecosystem function changed and fire regimes permanently altered. For example, the leguminous shrub *Mimosa pigra,* introduced from central America, is capable of increasing soil nitrogen levels in the wetlands of the Northern Territory as well as changing the habitat for waterbirds, such as the magpie goose (Braithwaite *et al.,* 1989). The introduced tree *Tamarix aphylla* or Athel Pine has changed river physiography and water flow of the Finke River in central Australia over about 20 years, since a major flood in 1974; this species is able to reduce regeneration of the native riverine vegetation and by accumulating salt *Tamarix* may permanently change the ecosystem (Griffin *et al.*, 1989). Many other examples could be given: Boneseed (*Chrysanthemoides monilifera*) from South Africa in coastal sand-dune communities, Rubber vine (*Cryptostegia grandiflora*) from Madagascar in Queensland watercourses, vine thickets and open-forest, and European blackberries (*Rubus fruticosus* agg. and other species) in open-forest gullies and along waterways of south-eastern Australia.

Introduced plants affect numbers of native plant species, floristic composition or the functioning of native vegetation in many ways. While there are many well-documented instances of introduced plants reducing economic value of agricultural products, there are only a few for introduced plants deleteriously affecting native plant biodiversity, ecosystem function and vegetation structure. It is a subject in urgent need of more research.

Plants do not need to be introduced from outside Australia to be weedy in natural vegetation, however. There are now many instances of indigenous plants becoming weedy when they move beyond their native range. The native shrub *Pittosporum undulatum* is indigenous to some subtropical moist gullies on the south coast of New South Wales and far eastern Victoria. Because of its perceived horticultural value, and especially its scented flowers, it has been widely planted beyond its fairly localised native range (Gleadow & Ashton, 1981). The increased rate of propagation of the shrub, its shade tolerance and the fact that its seeds are bird-dispersed has led to *P. undulatum* spreading widely; it is now a common and sometimes dominant species in many vegetation types in southern Victoria and South Australia where it never occurred 200 years ago.

A number of species naturally restricted in their distribution to Western Australia are now occurring as environmental weeds in eastern Australia, especially in coastal vegetation (for example, the plant known as Cape Wattle, Crested Wattle or Cape Leeuwin Wattle, *Paraserianthes lophantha*), and the reverse situation is equally common (for example, Tasmanian Blue Gum, *Eucalyptus globulus*). This enhanced admixture of native plant species has consequences for hybridisation within genera of Australian plants and untold effects on native plant function and survival.

Summary and conclusions

Australia is a vast continent that spans more than 30 degrees of latitude, over which average annual rainfall varies from less than 100 mm to more than 2000 mm and from summer- to winter-incident as latitude increases. Geologically, it is an old continent with nutrient-impoverished soils in many regions. This chapter has described the five major types and some subtypes of natural vegetation that occur over this diverse continent. Some of the ecological factors that may account for the patterning of those vegetation types have been discussed for different regions of Australia.

The present distribution of the different vegetation types is in no way constant over time, however, and never has been. As the continent separated from Gondwana and drifted northwards, shifts in palaeoclimates changed distribution patterns of vegetation types (Frakes, this volume). The arrival of Aboriginal people and their use of fire changed vegetation patterns in ways that we are only gradually becoming aware of. More recent clearance of native vegetation in many parts of Australia has often been excessive and ecologically disastrous; in southern Australia, at least, it has resulted in a general shift from deep-rooted perennial vegetative cover to one dominated by annuals, usually with shallower root systems. After 200 years of European exploitation, further clearance of natural vegetation has only recently been outlawed over most of Australia. Past utilisation of native vegetation, whether for grazing by domesticated stock or for timber, over the same period, has drastically reduced habitat for many native plant and animal species, with consequent loss of biodiversity, not all of which we even know about. Clearance and grazing along with ecologically inappropriate use of fire have together changed entire landscapes and rendered those landscapes susceptible to weed and pest invasion as well as to increased salt levels in surface- and ground-water. Urbanization of coastal regions progresses with seemingly few checks and balances, producing homogenisation of localised areas of natural vegetation and planted European-style gardens in the 'bushland' around the major Australian cities.

On the above basis, the scenario for the future of Australian vegetation is grim unless human population pressure on the land can be reduced. There are, however, some grounds for optimism. An increased percentage of land under reservation could lead to wiser land management, including the conservation of representative samples of the vegetation types and subtypes described above. Recently, there has been an increase in knowledge of these vegetation types and their dynamics, on which management programs for their conservation can be based. Whether this increase in knowledge translates into wiser land management remains to be seen. Increase in knowledge of the Australian flora should be accompanied by similar increases in knowledge of the unique Australian vegetation types and their variants. Given this more optimistic basis, conservation of a representative sample of such vegetation types should follow and lead thereby to an enrichment of the quality of life for future generations.

Acknowledgments

A previous draft of this chapter benefited greatly from comments by my colleagues Malcolm Gill, Jeremy Burdon and John Vranjic.

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THE AQUATIC FLORA

Certain preconceptions accompany any thoughts of the Australian flora. Our minds generally settle on visions of towering *Eucalyptus* forests, or *Banksia* heathlands, or the fields of colourful wildflowers that signal the onset of Spring. It is a natural – and entirely understandable – human response to appreciate the big and the brightly coloured. But as a result a significant portion of the Australian flora is often ignored. One group of plants that falls into this category is that which inhabits the aquatic environment. These plants are constantly or periodically immersed in either fresh or salt water, and as a result are largely hidden from view. With a few exceptions, their flowers are small and cryptic and do not make a great impression on the casual observer. Yet the aquatic environment hosts a vast diversity of plant species and their communities are of great ecological significance.

The aquatic environment is the ancestral home to all plants and, by and large, remains the domain of the algae. The algae found in Australian waters will be the subject of a independent series, the *Algae of Australia*, that will follow the *Flora of Australia* in general format, and, as such, will not be discussed here. The present chapter is concerned with the vascular aquatic plants and their habitats. Traditionally these have been studied as terrestrial systems (rivers, lakes, swamps and marshes) on the one hand, or marine systems (seagrass beds) on the other. In between, the transitional plants, the mangroves, have had their own suite of researchers. In practice, of course, such sharp distinctions do not, in many cases, exist on the ground, with one system merging gradually into another.

TERRESTRIAL WETLANDS AND WATERPLANTS

Surrey W.L. Jacobs[1]

Aston (1973) considers aquatic species 'to be those adapted to growing in or on permanent water, either completely submerged or emergent, and having a definite life form (habit, structure) related to this aquatic environment.' Sainty & Jacobs (1981) define waterplants as 'species which thrive in water or on wet land.' Mangroves can be either excluded (Aston, 1973) or included (Sainty & Jacobs, 1981), the decision usually being made on practical grounds. By convention, alpine plants are nearly always excluded from treatments of waterplants, simply because they are usually treated separately as a group of species defined by another set of ecological criteria (Costin *et al.*, 1979). These criteria are not mutually exclusive so usually there is a pragmatic decision made on membership of either category. Defining any group of species on ecological criteria is fraught with difficulty and may result in either pages of qualifications or exceptions.

A wetland is is 'land permanently or temporarily under water or waterlogged' (Jacobs & Brock, 1993), modified after Paijmans *et al.* (1985). Adam (1992) provides an insight into the kind of aspects/arguments involved in defining wetlands and both Alper (1992) and Stone (1995) provide good examples of the ecological chaos that can be perpetrated when law makers and benders start playing with words without understanding the significance of what they do. Pressure may be applied for stricter definitions but history tells us that any more specific definition of a wetland that does not incorporate consideration of its catchment or water source could well be abused. The most useful approach is to work on a very general definition and modify it as required to the particular project.

Ecological information on Australian wetlands has been reviewed for tropical Australia by Finlayson & Oertzen (1993) and for temperate Australia by Jacobs & Brock (1993). The conservation of Australian wetlands has been reviewed by McComb & Lake (1988) while preliminary analyses of the biogeography of Australian waterplants have been undertaken by Jacobs & Wilson (1996).

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[1] National Herbarium of New South Wales, Royal Botanic Gardens, Mrs Macquaries Rd, Sydney, New South Wales 2000.

Composition of the aquatic flora

This, of course, is dependent on the definition of 'aquatic' used. Jacobs & Wilson (1996) record 553 species in 139 genera in 56 families for Australasia. Aquatic bryophytes are few and mainly temperate. Ferns are present in about the same proportion as in terrestrial floras (Clarkson & Kenneally, 1988) and fairly evenly distributed with the exception of the south-west of Western Australia where there has been a proliferation of *Isoëtes*. There are no aquatic gymnosperms recorded for Australasia. The big difference between terrestrial floras and aquatic floras is in the proportion of monocotyledons: in regional aquatic floras the proportion of monocotyledons ranges from 50% to 70%, approximately twice the proportion represented in the total floras (20% to 30%). These are mostly in the families Cyperaceae and Poaceae, but there are also several specialised families of aquatic monocotyledons, such as Potamogetonaceae, Hydrocharitaceae, Nymphaeaceae, and others.

Adaptations to an aquatic environment

An aquatic environment imposes unusual conditions on plants. For example, waterlogging of root systems is common to all aquatic environments, and has engendered a range of adaptations; saline environments require adaptations to levels of sodium and choride ions that are fatal to most plants; and pollination in submerged or barely emergent flowers also requires different strategies to those found in terrestrial plants.

General adaptations to an aquatic environment

For many species of waterplants, the adaptations or complex of adaptations that allow them to have a competitive advantage in what can be a difficult environment are only now becoming understood. Problems not normally faced by terrestrial species, but which affect aquatic plants, include stability in a substrate not suited for strong root systems, photosynthesis where light energy levels are frequently low and leaf exposure to light may be limited by high flow rates, turbidity, floods and/or epiphytes, and pollination in an environment quite different from their ancestors. Sculthorpe (1967) supplied a comprehensive account of anatomical and morphological characteristics of waterplants while Jacobs (1985) provided a shorter summary. Falkowski & Raven (1997) discussed some of the physiological adaptations involved in photosynthesis in an aquatic environment, Carter *et al.* (1996) showed the effect of limiting light to submerged waterplants, Cook (1982) provided a fascinating discussion of some of the pollination mechanisms of the family Hydrocharitaceae, and den Hartog (1970) the pollination of seagrasses. Les *et al.* (1997) provided a survey of the incidence of hydrophily (water-moderated pollination mechanisms) and a cladistic study of the evolution of the trait(s), with particular reference to the Alismatidae.

Special adaptations to a saltmarsh environment

Saltmarsh species live in an extreme environment, although perhaps not as extreme as is sometimes imagined. Under 'dry' conditions the soils certainly contain extremely high levels of sodium and chloride ions. Most growth, however, takes place when the marsh is flooded by tides or floods. As the majority of saltmarshes are in estuaries, even tidal flushing can be with water substantially less saline than seawater. When saltmarshes are inundated by floods (as for example the large saltmarshes of tropical coasts), the water is often quite fresh.

Nevertheless, saltmarsh species have to survive long periods with high soil salinity. A very few species manage to avoid this by growing as ephemerals after inundation. This is most common in the tropics where seasonal flooding in the wet season allows species such as *Salsola kali*, *Sclerolaena* spp. and *Trianthema* spp. to complete their life cycles without being exposed to extremes of salinity.

Perennials are more common than annuals in saltmarshes, and most perennials use a combination of strategies that allow them a competitive advantage over other species in this environment.

The physiological variations that help in survival are discussed by Adam (1990). Examples include excretion (e.g. *Atriplex* spp., *Sporobolus* spp., *Zoysia* spp. and *Cynodon* spp.), variations in photosynthetic pathways, especially in the Chenopodiales (Carolin *et al*., 1975, 1978, 1982; Chapman & Jacobs, 1980) and grasses (Carolin *et al*. 1973; Brown, 1977), and tolerance of high levels of sodium and chloride ions. Frequently, ecotypes from a saltmarsh are able to tolerate higher levels of salinity than other ecotypes of the same species.

Succulence is often claimed to be of significance as an adaptation to salinity, but, as Adam (1990) pointed out, succulence is difficult to define and covers a multitude of characters. A certain level of succulence is induced by increasing salinity. It is sometimes suggested that this increase in succulence is to allow isolation of sodium and chloride ions in the vacuole, or to allow the accumulation of other compounds that help maintain an osmotic balance or pH balance (Adam, 1990). Succulence is often also associated with other features (for example Crassulacean Acid Metabolism (CAM)), and it is not clear how it directly relates to enhanced survival in saline conditions.

Special adaptations to a marine environment

The adaptations of mangroves to an intertidal environment, and of seagrasses to a subtidal environment, are discussed separately below, by Bridgewater and Walker respectively.

Classification

Systematics

Aquatic plants occur in many families and there are more species in non-specialised aquatic families than in specialised aquatic families. While the taxonomy of waterplant groups is about as stable as that for many other groups, there are problems that are unique to some strictly aquatic families. The highly reduced and modified flowers of species of Zosteraceae, Najadaceae, Zannichelliaceae and others means that the interpretations of the floral structure vary. As this is often important in understanding relationships, it is the increasing understanding of floral structure that has been primarily responsible for changes in classification between, for example, den Hartog (1970) and Dahlgren *et al*. (1985). The system used in the *Flora of Australia* for the aquatic monocotyledon families is that of Cronquist (1981). This differs slightly from the more recent classification of Dahlgren *et al*. (1985) in that Cronquist recognises Ruppiaceae as distinct from Potamogetonaceae, includes Scheuchzeriaceae in Juncaginaceae, includes Butomaceae in Limnocharitaceae, and places Aponogetonaceae in Order Najadales instead of Order Alismatiflorae. There is no 'final' classification on the horizon. The process of increasing knowledge means that pre-existing classifications will be modified periodically as data accumulate. Classifications of this type are a method of storing and retrieving information and, usually, constructed to reflect evolution and hypothesised relationships. They are hypotheses in their own right and are testable.

Wetlands classification

Ecological classifications are of a different nature to taxonomic classifications. They are usually based on comparatively simplistic characteristics of either the plant (e.g. growth form), physical habitat or climate. There are no evolutionary connotations in such classifications and they are usually constructed with a specific project in mind. They are usually not established as hypotheses and are therefore not testable. It is often assumed from experiences with terrestrial vegetation and plant communities that all plant communities are stable entities. While this is not even strictly true for all terrestrial communities (e.g. the so-called 'fire-weeds'), it is certainly not true for aquatic plant communities.

The simplest ecological classification of wetland plants is based on growth form and behaviour, and includes character combinations such as:

(i) rooted, submerged, flowers submerged;

(ii) rooted, submerged, flowers emergent;

(iii) free-floating submerged, flowers submerged;

(iv) free-floating on surface;

(v) rooted, leaves floating, flowers emergent;

(vi) rooted, leaves emergent, flowers emergent;

(vii) woody trees or shrubs.

There are many examples of these and the number of categories usually depends on the number of species in each category for each study. Such a classification is useful for easy grouping prior to species identification or habitat categorisation. Examples of the use of such a system are in Sainty & Jacobs (1981, 1994).

Australian wetlands have also been classified on the basis of geographical and/or physical features (Jacobs, 1983; Riley *et al*., 1984; Paijmans *et al*., 1985), the structure of the vegetation (Briggs, 1981; Blackhall, 1986) or a mixture of both (Riggert, 1966; Beadle, 1981; Norman & Corrick, 1988). Reviews of classification systems are provided by Jacobs & Brock (1993), Sainty & Jacobs (1994) and Finlayson & Oertzen (1993).

Most classifications were developed as part of localised studies, often within political rather than phytogeographical boundaries, and hence they tend to rely heavily on characteristics important to that particular study. For example, many studies of birds concentrate on vegetation structure as the basis for habitat classification (e.g. Blackhall, 1986) whereas De Deckker (1982) uses the relative suitability of wetlands as sites for palaeolimnological investigations.

Classifications of wetlands relying on vegetation structure and floristics are often difficult to adapt to larger scale studies. The degree of precision involved when genera or species, or percentage cover or growth form are involved in the definitions, means a lack of flexibility that often requires change in the classification of a particular wetland after flood, drought or fire (all common in the Australian climate). Most wetland vegetation types are subject to more frequent change than most dryland types. In many ways they are more similar to ephemeral dryland plant communities than to more perennial types.

The number of final categories in the classification is also important for practical reasons. Briggs (1981) has 45, Paijmans *et al*. (1985) has 55 and Beadle (1981) 58. Riley *et al*. (1984) produced a precise geomorphological hierarchical classification for the wetlands of New South Wales. With seven levels in the hierarchy and more than 1500 possible final categories it is far too finely divided to use for biological data. Even if only the top five levels of the hierarchy could be used there are about 150 categories.

The system used here (Jacobs, 1983) is based on geographical and physical characteristics and is one of the simpler systems. It was developed as a means of summarising data from numerous different sources and is especially useful for Australian wetlands and as a base for elaboration for detailed studies. References and more detail are in Jacobs & Brock (1993) and Finlayson & Oertzen (1993), and references included below are additional to those in the earlier publications. The classification is:

1. Coastal wetlands
   (a) upland swamps
   (b) rivers and tributaries
   (c) floodplain swamps and billabongs

  - (d) coastal lagoons and lakes
  - (e) estuaries
    - (i) mangroves
    - (ii) seagrass meadows
    - (iii) salt marsh

2. Mountain lakes and swamps
  - (a) perennial lakes
  - (b) perennial swamps
  - (c) ephemeral lakes/swamps
3. Inland rivers
  - (a) rivers
    - (i) perennial, including anabranches
    - (ii) ephemeral
  - (b) billabongs and floodplains
  - (c) swamps – overflow or terminating
4. Inland lakes
5. Mound springs
6. Man-made storages, canal systems, dams, channels, drains, bores, bore-drains, farm storages, rice fields, storage swamps.

Descriptions of wetland types

1. Coastal wetlands

(a) Upland swamps

Upland swamps are most common along the eastern Great Dividing Range but are also found in the Kimberley, Western Australia, and other upland areas. They are situated at the heads of the coastal rivers. Many often do not have free-standing water but may absorb large volumes of water in the peat-like accumulations of organic matter. This water is released slowly, helping to maintain flow in tributaries. These upland swamps differ from the rest of the wetlands, often being described simply as wet heaths and having more in common with the surrounding dryland vegetation and fauna than with that of other wetlands. The vegetation of the swamps includes a large proportion of monocotyledonous genera from the families Cyperaceae and Restionaceae, commonly including *Baumea*, *Gahnia*, *Lepidosperma* and *Gymnoschoenus* (Cyperaceae) (Fig. 114), and *Leptocarpus* and *Lepyrodia* (Restionaceae). Other components include species of *Melaleuca* and *Leptospermum* (Myrtaceae), *Hakea* and *Banksia* (Proteaceae), and *Epacris* and *Leucopogon* (Epacridaceae). Stricker & Stroinovsky (1995), and Stricker & Wall (1995) provide recent assessments of some of these wetlands around Sydney, New South Wales.

(b) Rivers and tributaries

There are rivers all along the coast except for areas of Western Australia. Although water from the Murray-Darling System reaches the coast, the rivers and tributaries of this system are classified as inland rivers. Where the flow rate is high there is usually little characteristic vegetation in or around the channels. The vegetation of the banks is mostly dependent on the local soil type and the rainfall of the country through which the rivers flow. As the river channels broaden, the slope lessens, the flow rates decrease, more alluvium is deposited and the nutrient content of the water increases.

Typical submerged plant species in these rivers include *Blyxa* spp. and *Hydrilla verticillata* in the north, along with *Vallisneria* spp. and various species of *Potamogeton*. Free-floating species or species with floating leaves are not common. River banks are frequently lined with emergent species such as *Phragmites australis, Bolboschoenus fluviatilis, Schoenoplectus mucronatus, S. validus*, *Triglochin* spp. and *Persicaria* spp. The banks themselves are frequently heavily wooded with rainforest-like fringing woodlands or *Melaleuca* spp.

Australia's only two species of Podostemaceae (*Tristicha* and *Torrenticola*) grow as submerged plants in fast-flowing upper reaches of a few rivers in Queensland, Northern Territory and Western Australia.

(c) Floodplain swamps and billabongs

These wetlands are the most diverse in both the structure and composition of their vegetation. The word billabong is of Aboriginal origin and is used in Australia to describe permanent or semi-permanent areas of open water on riverine floodplains. On inland rivers they are often oxbows.

Many floodplains and billabongs have been modified or completely obliterated by alteration of water level, grazing, draining, and reclamation. They also receive increased nutrient loads from urban and rural developments in their catchments and support a large number of introduced species.

The shallow wet areas of these lowlands are often dominated by trees of *Melaleuca* spp. with an understorey dominated by sedges (Cyperaceae) and species of Restionaceae. Common understorey genera include *Caustis*, *Fimbristylis*, *Schoenus*, *Baumea*, *Callistemon* and *Banksia*. Northern billabongs frequently have a rich flora in deeper water including *Nymphaea* spp. and the Lotus, *Nelumbo nucifera*, as well as several grasses (e.g. *Pseudoraphis* spp., *Leersia* spp., *Oryza* spp.), *Nymphoides* spp., *Marsilea* spp. and *Eleocharis* spp. (Figs 119, 120).

Submerged plants of *Utricularia* spp., *Hydrilla verticillata* and *Vallisneria* spp. are common in the north, with *Vallisneria americana* and *Potamogeton* spp. common in the south.

Floating plants of the two species of *Azolla* and several species of Lemnaceae (in the genera *Lemna*, *Wolffia* and *Spirodela*) are common over most of Australia. *Pistia stratiotes*, now introduced elsewhere in Australia, was previously only common in the large floodplain swamps of the Northern Territory.

(d) Coastal lagoons and lakes

Several different types of lakes are identifiable depending on how they were originally formed. They are not very common in the tropics. Lagoons or lakes that are frequently open to the sea have a submerged vegetation of *Zostera capricorni* which, in the south, is replaced by *Z. muelleri*. Other lagoons in the south usually have *Ruppia* spp., charaphytes (e.g. *Chara* spp. *Nitella* spp., *Lamprothamnion* spp.) or, along the southern coasts, species of *Lepilaena*. The edge communities, when present, usually consist of emergents such as *Phragmites australis, Juncus kraussii, Bolboschoenus* spp. and *Schoenoplectus* spp.

(e) Estuaries

Estuaries have been reasonably well-studied and the vegetation can be divided into: (i) saltmarshes, (ii) mangroves, and (iii) seagrass meadows.

i. Saltmarshes. Saltmarshes are frequent on low-lying areas near saline water or mangroves. Coastal saltmarshes are usually subjected to periodic flooding, often by tides. They differ from mangroves in generally not being dominated by trees, but Australian temperate saltmarshes may have quite substantial numbers of *Casuarina* spp, which are not normally regarded as mangroves. Good general accounts of saltmarshes can be found in Beadle (1981), Adam (1981) and Hutchings & Saenger (1987).

While there has not been the same detailed study of the biogeography of Australian saltmarsh species as there has been for other aquatic plants (Jacobs & Wilson, 1996), there seems to be an obvious distinction in species content between tropical and temperate saltmarshes. This is masked to some extent by the almost ubiquitous *Sporobolus virginicus*, which becomes even more common in tropical saltmarshes. Common temperate saltmarsh species include *Sarcocornia quinqueflora*, *Halosarcia* spp., *Zoysia macrantha*, *Samolus repens*, *Suaeda australis*, *Juncus kraussii*, *Selliera radicans*, *Tetragonia tetragonioides* and *Triglochin striata*. Grasses are relatively uncommon in our temperate saltmarshes, but *Distichlis distichophylla*, *Puccinellia stricta* or *Austrostipa stipoides* may be locally common. *Casuarina glauca* (in the east) or *C. obesa* (in the west) may grow in and/or on the landward margins of the marsh. South Australia has very large areas of coastal saltmarsh that merge into more inland saline communities dominated by species of Salicornieae and other chenopods, and some genera of Aizoaceae such as *Disphyma*, *Carpobrotus* and *Gunniopsis*.

Tropical saltmarshes can be harder to define than their temperate counterparts. The mangroves may be much more intermittent and there may be large saline flats that are only rarely inundated and then mainly by floodwater. Some of these saline flats may seasonally support large stands of grasses such as *Xerochloa* spp. and be bare for much of the year, or have occasional shrubs of *Halosarcia* spp. More regularly inundated sites may be dominated by the grass *Sporobolus virginicus*. Other common species include *Suaeda arbusculoides*, *Tecticornia* spp., *Sesuvium portulacastrum*, *Sclerolaena bicornis*, *S. glabra*, *Salsola kali*, *Trianthema* spp. and *Zaleya* spp.

ii. Mangroves. Mangrove communities are tidal forests, occupying the boundary between land and sea. They cover about 11 550 sq km of the Australian coastline, with the main areas found in the tropics (Galloway, 1982). Species richness is also greatest in the tropics, declining to a monospecific community (*Avicennia marina*) in the south of the continent, in Victoria, South Australia and Western Australia. No mangroves extend to Tasmania. In north-eastern Queensland on the other hand, there are about 30 mangrove species, with the genera *Bruguiera* (5 spp.), *Rhizophora* (4 spp.), *Sonneratia* (4 spp.), *Lumnitzera* (3 spp.), *Xylocarpus* (3 spp.), *Avicennia* (2 spp.) and *Ceriops* (2 spp.) supplying the largest numbers of taxa (Busby & Bridgewater, 1986). Numbers decline steadily with increasing latitude (and decreasing mean temperature). Mangrove communities are typically devoid of an understorey, although on their landward side they frequently grade into saltmarsh. Mangrove communities are discussed in more detail in this volume by Bridgewater (below), and by Adam (1994).

iii. Seagrass meadows. Australia has about 30 of the world's 58 species of seagrasses, as well as some of the most extensive seagrass meadows. All six families (Hydrocharitaceae, Posidoniaceae, Cymodoceaceae, Zannichelliaceae, Ruppiaceae and Zosteraceae) are represented here, as well as 13 of the 14 genera. Seagrass meadows occur from tropical to cool-temperate regions, and are characteristic of calm, sheltered, shallow waters such as embayments and lagoons. They are discussed in more detail in this volume by Walker (below).

2. Mountain lakes and swamps

(a) Perennial lakes

Australia has comparatively few upland perennial lakes and these rarely develop a characteristic flora. The lakes are mostly shallow and subject to large fluctuations in area and depth. Consequently, most have few submerged species and those that do grow are adapted to seasonal water-level fluctuations. The most common species in the lakes are *Ruppia megacarpa*, *Vallisneria* spp., *Lepilaena* spp. and *Myriophyllum* spp. Marginal emergent vegetation is not well-developed and is usually restricted to the hardiest species, such as *Phragmites australis*, *Typha* spp., and members of the Cyperaceae, possibly because of wave action. Algal blooms are common in such lakes, especially where they are surrounded by agricultural land. Most of these lakes are found in the south-east, the Murray-Darling Basin, and in Tasmania. Benson & Jacobs (1994) have surveyed and classified the perennial and ephemeral lakes of the Monaro region of New South Wales. The lakes in the tropics are mostly a result of volcanic activity and usually have a rich sedge flora (e.g. *Eleocharis* and *Cyperus*) and species of *Nymphaea* and *Nymphoides*.

(b) Perennial swamps

Perennial swamps in the higher country are similar to coastal swamps in species composition but generally support more species of the families Cyperaceae and Juncaceae as well as species of *Ranunculus*, *Villarsia*, *Glossostigma*, *Limosella*, *Myriophyllum*, *Lythrum* and *Montia*. They occur along the Great Dividing Range and adjoining high altitude areas. In the tropics, where they are common, they are usually surrounded by species of *Melaleuca*, and have a species-rich understorey of grasses and sedges. Any areas of deeper water have floating-leaved emergent species of *Nymphaea*, *Nymphoides* or *Marsilea* and submerged species of *Vallisneria*, *Blyxa* or *Utricularia*.

(c) Ephemeral lakes/swamps

These wetlands can be difficult to distinguish from their more perennial counterparts. Many are ephemeral on a long term cycle (e.g. 10–15 years) and the dry period is probably an important factor in determining differences between their communities. The longer-cycle ephemeral wetlands are superficially similar to their perennial equivalents; the short-cycle ones usually support more plant species, although sometimes the whole area is largely covered with one species of *Amphibromus*, *Eleocharis*, or species of the family Cyperaceae. Occasional aquatic species are often present all year but if the area is heavily grazed (as is frequently the case) then the composition of the vegetation may differ dramatically at different periods of inundation. Ephemeral swamps in the tropics often have scattered trees of *Melaleuca* spp. (frequently *M. viridiflora*) and a sedge- and grass-rich understorey. Common genera include *Eriachne*, *Sacciolepis*, *Fuirena*, *Scleria* and *Drosera*.

3. Inland rivers

There are three types of inland riverine systems: (a) rivers, (b) billabongs, and (c) swamps. Three Drainage Divisions (Murray-Darling, Bulloo-Bancannia, and Lake Eyre) (Australian Water Resources Council, 1976) have rivers whose origins are in areas of comparatively high rainfall and then flow inland through areas of lower rainfall. Only from the Murray-Darling does some water actually reach the sea.

(a) Rivers

(i) Perennial rivers, including anabranches. Only the Murray-Darling Drainage Division includes true perennial rivers although the Lake Eyre Division has some that are perennial in their headwaters. Towards their source, perennial rivers are lined with *Casuarina cunninghamiana* and support submerged aquatics like *Vallisneria* spp. or *Potamogeton* spp. Emergents including *Typha* spp., *Phragmites australis*, *Triglochin* spp. or *Eleocharis* spp. grow in protected sites. After the rivers meet the plains, the channels are characteristically lined with *Eucalyptus camaldulensis*, *E. microtheca s. lat.* or *Melaleuca* spp., with a scattering of *Acacia stenophylla* or *E. largiflorens*. The water becomes turbid from suspended soil particles and dissolved organic matter by the time it reaches the plains. The reduction in light penetration, coupled with fluctuating levels and flows, means that few submerged aquatic species grow in the river channels. The anabranches, with their less rapidly fluctuating flows, may support sparse populations of submerged aquatics like *Vallisneria* spp., *Myriophyllum verrucosum* or *Potamogeton* spp., as well as patches of emergents such as *Typha* spp. and *Phragmites australis*. There is some circumstantial evidence that changes to the riverine environment caused by European man have been responsible for the rapid spread of European Carp and large decreases in the amount of submerged macrophytes.

(ii) Ephemeral rivers. Many ephemeral rivers only carry water for short periods after rain, with a few shallow pools persisting longer. Others, with catchment heads in higher rainfall areas, have almost permanent headwaters, but are ephemeral for the majority of their length with occasional more perennial waterholes. The channels are usually lined with *Eucalyptus camaldulensis* (Fig. 100), *E. microtheca*, or *E. largiflorens*. Aquatics are confined to the more permanent pools. The more permanent the pool the greater the range of aquatic species. As in perennial rivers, *Potamogeton* spp., *Myriophyllum* spp. and *Vallisneria* spp. are the more common submerged aquatics, but there is usually a greater range of emergents with

species of *Cyperus*, *Eleocharis, Persicaria* and *Juncus* in addition to those found in perennial rivers. Algal blooms are common when nutrient levels rise as the water levels fall.

(b) Billabongs and floodplains

Billabongs of inland areas are oxbows or river bends. They are often quite deep, fill during floods, and dry slowly. Plant species are similar to those of the main rivers but emergents are more common. *Muehlenbeckia florulenta* often grows on the banks. If domestic stocking rates are not too high, *Ottelia ovalifolia* or one of the floating-leaved species of *Potamogeton* may grow in the shallow water. Edge communities of species such as *Damasonium minus*, *Marsilea* spp., *Crinum flaccidum*, *Sporobolus mitchellii*, and strand species such as *Heliotropium curassavicum* or *Glinus lotoides* may also establish.

(c) Swamps – overflow or terminating

Some inland rivers only flow right through to the next channel during major floods; most of the time they terminate in ephemeral lakes, large swamps or playas. Others may overflow in large floods, inundating huge areas (sometimes in excess of 100 km^2). Normally the Lachlan River terminates in the Great Cumbung Swamp in southern New South Wales, the Macquarie River in the Macquarie Marshes in western New South Wales, and the Bulloo River before the Bulloo Overflow on the New South Wales/Queensland border. The Bulloo Overflow fills only occasionally and the water may take ten years or more to disappear. When full, many swamps have large expanses of turbid, shallow water and wave action and turbidity usually limit submerged vegetation. As the water levels drop, a ground cover of species of *Marsilea*, *Cyperus*, and *Eleocharis* develops with *Atriplex* spp. and *Eragrostis australasica* in the marginal depressions. Stands of *Muehlenbeckia florulenta*, *Eucalyptus microtheca* or *E. largiflorens*, or *E. camaldulensis* develop along the deeper channels.

4. Inland lakes

Inland lakes are mostly ephemeral. Some are seasonally ephemeral, others flood irregularly and some may remain full for many years before drying. Some perennial lakes occur in the wetter regions of the south.

Many of the lakes are terminating (endorheic); some form the source of rivers (exorheic). They range from fresh to quite saline. Wave action and fluctuating water levels limit the vegetation in larger lakes but species of *Ruppia*, *Lepilaena*, and *Lamprothamnion* are reasonably widespread. The immediate areas draining into these lakes usually support swamp species such as *Eucalyptus camaldulensis*, *Muehlenbeckia florulenta* or *Eragrostis australasica* if the salinity levels are not too high, and species of Chenopodiaceae (especially Salicornieae) and sometimes *Muehlenbeckia coccoloboides* for lakes of higher salinity.

These lakes are varied, including crater lakes, spring-fed lakes, and lakes fed from local run-off. The last group may start as essentially fresh, becoming increasingly saline as the season progresses; others are only ever saline but their salinity increases as the water level falls.

The Lake Eyre Drainage Division has the largest, most spectacular, and most intermittent of the inland saline lakes. On the rare occasions when these lakes fill they support abundant life until the salinity levels increase. When partially full the salinity levels are often too high for plant and animal life but apparently the salinity can be quite variable.

5. Mound springs

Mound springs form a minute percentage of wetlands yet they represent (or represented) the only permanent and reliable water source in much of the drier regions of the Murray-Darling, Bulloo-Bancannia, and Lake Eyre Drainage Divisions. Other mound springs, not all associated with the Great Artesian Basin, occur in Western Australia. The South Australian mound springs have been surveyed by Greenslade *et al*. (1985). Mound springs are natural outlets of the Great Artesian Basin, one of the largest artesian basins in the world with an area of about 1.8 million km^2. They are usually associated with fractures and fault lines and often have mounds of various sizes. Some of the extinct springs have mounds of several square kilometres. The mounds are built up from the minerals precipitated from the springs; the weaker the spring the larger the mound tends to be. The salinity of the water varies, as does the rate of flow. Most of the springs are used by stock, feral and native animals, and well-developed vegetation and larger surrounding wetlands were common before artesian bores were drilled and stock introduced. Uncontrolled artesian bores have apparently been responsible for lowering the water levels and pressures in the Basin, thereby reducing the amount of water reaching the surface. Rates of flow in mound springs are decreasing, and many have ceased flowing altogether. Recent moves to cap and control the flow from bores does seem to be having some positive effects for mound spring flows. The southern mound springs characteristically have species such as *Cyperus gymnocaulos*, *C. laevigatus*, *Schoenoplectus pungens*, *Typha domingensis* and *Phragmites australis*, with a few other species appearing less commonly. A few species are endemic to mound springs, including *Eriocaulon carsonii* and an undescribed species of *Utricularia*.

6. Man-made storages, canal systems, channels, drains, bores, bore-drains, farm storages, rice fields, storage swamps

Positive effects of man-made storages include the increase in numbers of large kangaroos since European settlement, largely due to the installation of a much more reliable network of watering points across the country. The range of a number of native plants have extended by colonisation of dams and other artificial water storages. Examples are *Myriophyllum verrucosum* in arid Australia (Orchard, 1986) and *M. variifolium*, *M. simulans*, and related species in wetter areas of south-eastern Australia. On-farm storages also provide habitats for waterbirds. Those species that are hunted are undoubtedly aided by an increase in number and dispersion of suitable habitats. The waterbird populations on artificial waterbodies depend largely on the age, size, and depth of the wetland. The types and extent of particular habitats are important. Those with an array of depths and plant communities have rich invertebrate communities and more waterbird species (Broome & Jarman, 1983).

The plants in these artificial wetlands, which occur all over the country, vary greatly. The species composition reflects both geographical region and the management of the particular wetland. Although many different species grow in man-made storages, less common plant species rarely seem to benefit. For example, *Eriocaulon carsonii* and *Utricularia* sp., endemic to mound springs, have not yet been recorded from any artesian bore or bore drain.

Biogeography

Jacobs & Wilson (1996) investigated the biogeography of Australasian waterplants and concluded that there is a major disjunction between the temperate and tropical aquatic floras. This distinction is more clearly defined at the species and genus levels than at the family level. A second important determinant in the differences/similarities appears to be the distance between the wetlands, although there also appears to be a strong relationship with the migratory flight paths of trans-equatorial birds (Lane, 1987).

Jacobs & Wilson suggest that Australia's aquatic flora has developed through a combination of distance dispersal, vicariance and local speciation. Climate is thought to be the most significant vicariance barrier at the species level. The geographically closer the areas are within either the tropical or temperate zones the more similar their floras are. This similarity is maintained by distance dispersal of species. At the generic level the climatic and distance barriers seem to have been about equally important. At the family level the situation is less clear, but it appears that the physical barriers have been more important than the climatic ones.

The similarity between aquatic floras of different continental areas has been noted and commented on by others. Thorne (1972) notes that more than half of his 'subcosmopolitan' category of genera are aquatic and, of the very few species that can be described as subcosmopolitan, nearly all are aquatic. Kloot (1984) notes that 61 of the 98 native species considered to have disjunct natural distributions between southern Australia and other temperate regions of the world are aquatic (the largest group of the remainder represent taxonomic errors).

The decline of wetland quality

In the past 100 000 years Australia has gone through wet and dry periods, presumably with corresponding fluctuations in waterplant populations. During this same period, Aborigines used fire to change the populations of dryland plants but, apart from harvesting some species for food, probably had relatively little impact on the waterplants. In the last 200 years European colonisation has had an enormous impact on vegetation in Australia.

Although we can be reasonably sure of the composition of the terrestrial vegetation around the watercourses at the time of European colonisation, we have very little idea of what was in the rivers themselves. By talking to people with long associations with waterways and collating their stories with what we see today, we can develop theories or hypotheses. Unfortunately these cannot be tested easily, only compared with future observations.

The deterioration of waterplant numbers and water quality started at Botany Bay. By the early 1800s the seagrasses in the bay were reduced by disturbance of the bed during harvesting of mud oysters. The Cooks River, a stream that now enters Botany Bay by an artificial route near the main runway of Kingsford Smith airport, Sydney, was classed as polluted and unfit for human use by the mid-1800s (McGuinness, 1988; Sainty & Jacobs, 1994). Since then many other streams, estuaries and wetlands have deteriorated or been destroyed.

The causes of deterioration are many. Land clearance for agriculture caused erosion and increased run-off, bank vegetation diminished and stock had increased access to streams causing further erosion. Dams were built, water stored and released at different times of the year and at different temperatures to natural flows. Concrete 'creeks' were built to speed water on its way, adding to its velocity and erosive capacity. Cities and towns grew and government, industry and agriculture often allowed or deliberately directed effluent to discharge into wetlands, streams, bays, estuaries and the sea. Sainty & Jacobs (1994) estimate that, for example, less than 5% of the wetlands of south-east South Australia are untouched by a drainage system and more than 70% of the once extensive wetlands of the Swan Coastal Plain of Western Australia have been altered or obliterated in the last 150 years.

One of the symptoms of the changes, a direct response to the increase in nutrient levels, is the 'bloom' phenomenon. Any species can 'bloom' but the term is normally associated with a free-floating species that is suddenly able to colonise in large numbers areas that it was unable to occupy previously. Examples include the growth of the free-floating *Salvinia molesta* over 330 ha of Lake Moondara, Queensland (Finlayson & Oertzen, 1993) and the floating-attached *Alternanthera philoxeroides* on the Georges River, New South Wales (Sainty & Jacobs, 1981).

Public attention has been drawn to blooms because of the involvement of one group of organisms in particular, the blue-green algae or Cyanobacteria, that are capable of producing offensive odours and/or toxins poisonous to humans and stock. Blue-green algal blooms have always been a part of the Australian environment. In areas where water levels naturally dropped through evaporation and consequently nutrient concentrations increased, blooms were to be expected. These conditions were often met in our inland rivers and billabongs. By decreasing the amount of water now reaching these systems, and increasing the amounts of nutrients entering the systems, we are now seeing an increase in frequency, duration and distribution of blooms. Entwisle *et al.* (1997) gives a good entry into distinguishing different types of freshwater algae and their characteristics, with references. Jones (1994) provided a discussion on blue-green algae or Cyanobacteria, and the conditions thought to lead to blooms.

Increasing salinity in the basins of the inland rivers is having an adverse effect on some wetlands and waterplants. The problem is not new and was predicted, in part, by Baldwin *et al*. (1939) from a study of irrigation in northern Victoria. Unfortunately their prediction was ignored.

Salinity problems are often divided into dryland and non-dryland salinity. The division is artificial. The problem is a result of rising water tables, the commonest causes of which are:

- the clearing of deep-rooted perennial dryland vegetation and replacing it with shallow-rooted short-lived pasture species or annual crops;
- continued application of irrigation water over a comparatively small area, especially in places that historically have been subjected to naturally low levels of rainfall; and
- failure to return excess irrigation water to rivers, but leaving it to evaporate and/or add to the water table.

In practice, none of these factors operate in isolation. Macumber (1990) provides a good summary of current problems and Close (1990) describes the significance of the prehistory of the Murray-Darling Basin in making it particularly susceptible to salinity problems.

Ecological and environmental importance

Waterplants have often become a management and/or environmental issue where streams or waterbodies have been modified or created. The absence or presence of waterplants, including algae, can be used for assessing the health and status of the waterbody. The role of waterplants in maintaining ecosystems, the consequences of disturbance of the natural balance, and some suggested remedies, are discussed in detail in Sainty & Jacobs (1994).

Submerged waterplants:

(i) reduce erosion by:

(a) reducing flow rates

(b) trapping suspended sediment;

(ii) add dissolved oxygen that supports much of the aquatic fauna and speeds the killing of harmful pathogens;

(iii) provide food either directly or indirectly for aquatic animals (including invertebrates) and a large number of terrestrial animals;

(iv) strip nutrients from water, and compete with bloom-forming algae for nutrients;

(v) provide a suitable physical habitat for the breeding of some aquatic animals;

(vi) help maintain habitat diversity and, therefore, total species richness.

Emergent, bank and floating plants:

(i) stabilise stream and lake banks;

(ii) provide food and shelter for aquatic animals;

(iii) provide habitats for the micro-organisms that improve water quality;

(iv) in some circumstances reduce evaporation;

(v) help to strip nutrients from water and sediments;

(vi) reduce turbidity by slowing flow, causing suspended matter to settle;

(vii) impart visual appeal to a waterbody.

Wetlands as a whole do all of the above. They also lower water velocities, thus reducing erosion and decreasing the height and velocity of a flood, but increasing its duration. In addition they provide:

(i) habitats for animals that live there;

(ii) water and food for animals from surrounding habitats;

(iii) refugia for animals that normally live under drier conditions;

(iv) staging areas for migratory or nomadic animals, especially waterbirds.

Economic Importance

The economic importance of wetlands is directly related to some of their attributes listed above. For sustainable long-term maintenance of agriculture and urban areas it will be necessary to carefully manage our biological resources. For most of Australia, and in particular those areas contributing the most to agriculture and with the greatest population, water is a major limiting resource. Australia has reached a stage where water exploitation by some user groups is having a deleterious effect on other user groups. Traditionally in Australia major (short-term) economic considerations have prevailed, but the importance of managing our resources sustainably, and the consequences of not doing so, mean that wetlands are beginning to receive recognition appropriate to their economic importance. This is true for things like water quality for both irrigation and drinking, reducing erosion, maintaining habitat diversity and species richness, and meeting some of our obligations to future generations in terms of sustaining both long-term agriculture and habitat diversity. Inventories of existing wetlands are being made, and their conservation status assessed (Usback & James, 1993; Australian Nature Conservation Agency, 1996).

In fact, the pendulum is now swinging in the opposite direction, with the role of wetlands in improving water quality becoming a fashionable touchstone. This has led to a proliferation of constructed wetlands, often built with unreasonable expectations. Sainty *et al.* (1994) provide a brief outline of some of the potential of consructed wetlands as water purifiers and common mistakes made in their construction and operation, Jacobs *et al.* (1995) assess performance of some of the species commonly used, Hunter & Claus (1995) describe some of the better early results that may be expected, and the papers published by the Queensland Department of Primary Industries (1995) outline the current range of attempts and results being achieved in this area. There are still very few records showing long-term benefits to water quality of constructed wetlands in Australia, but these may be expected as techniques improve.

Conservation

While it will never be possible to return all wetlands to their 'original' state, we can protect some of the remaining best examples and modify our actions to reduce adverse impacts on others. Some of the simpler remedies are listed below, and are considered in more detail in Sainty & Jacobs (1994):

(i) Increase main stream flows and limit diversions, aiming for a reduction of no more than 10%. More water must be allocated for the stream itself; a realistic whole catchment approach is the only hope for many of our river systems.

(ii) Modify old dams to allow water to be taken from different levels (to minimise the impact of cold water from the bottom of the storage on communities downstream). Newer dams often have the capacity for draw-down from different depths.

(iii) Reduce the amount of water extracted and increase efficiency in both on-farm storage and water use so that there is less loss from evaporation and less waste water.

(a) Drip or spray irrigation are good options for many crops, rather than more wasteful flood irrigation.

(b) Excess water should be re-used or treated and cleaned before being returned to the main stream.

(iv) Terminal 'swamps' or evaporating basins should be abandoned unless coupled with a managed system for physical salt removal, as they remove water from the main streams and add substantial amounts to the groundwater, exacerbating salinity problems.

(v) Buffer zones along streams can be built and maintained by fencing and controlling stock access.

(vi) Increased efforts are required to control European carp which increase turbidity and prey on native fish and other fauna.

Conservation has to be synonymous with total catchment management. It is not useful to isolate, even in thought, individual wetlands and streams from the total catchment (including groundwater). Although much lip service is paid to the concept, not enough happens yet in a practical sense, most catchments having several different facets controlled by different government agencies or departments. Catchment trusts are being formed (for example in Western Australia on the Swan Coastal Plain, on several major streams in Victoria, and the Hawkesbury-Nepean catchment Management Trust near Sydney). McComb & Lake (1988), Usback & James (1993) and Australian Nature Conservation Agency (1996) assess the conservation situation and provide information on the 'more important' wetlands (including Werribee Sewage Farm near Melbourne, Victoria!). Many of the remaining wetlands are physically protected (in quantity and quality), but the water supply of many of them is not.

MANGROVES

Peter Bridgewater[1]

Mangroves have long fascinated ecologists interested in coastal communities. There are perhaps 50 species of mangrove in Australia, and less than 200 world-wide. Yet there is little agreement on which plants are mangroves, and which are not. Workers in Australia have variously cited 45 taxa (Bunt *et al.*, 1982), 38 species (Busby & Bridgewater, 1986), 40 species (Smith & Duke, 1987) and approximately 30 species of trees and shrub (Hutchings & Saenger, 1987). Using a slightly broader definition, Wightman (1989) recognises 48 species for the Northern Territory. The problem stems from mangroves being a group of plants growing at the land/sea interface, with their roots literally in the water. Depending on the author, climbers, ferns and chenopods may or may not be included.

Mangrove forests (better described as mangal, following the pioneering work of Macnae, 1968) are highly productive ecosystems (Figs 121, 122), of major ecological significance for their nursery role in fish and invertebrate populations. Litter from mangal systems is also an energy source for benthic systems immediately off-shore. Galloway (1982) estimates the coverage of the Australian coastline by mangal to be 11 550 square kilometres.

Mangroves have a variety of unusual strategies to deal with their unusual environment. Because they are typically found in waterlogged anoxic soils, and are buffeted by tides which have large daily ranges (up to 9 m in north-western Australia), mangrove species have developed a variety of specialised root systems. These include the pneumatophores of the genus *Avicennia*, where roots grow upwards from the radial root system, and are alternately bathed in seawater, or exposed to air. *Bruguiera* species typically have 'knee' roots, where the root emerges, but then returns below substrate level. *Rhizophora* species have both pneumatophores and a system of stilt roots, which perform both a supporting and aeration role. Species typical of the landward part of the mangal, such as *Ceriops, Heritiera* and *Xylocarpus* have the typical buttressed root systems of rainforest species. All these root systems have a large amount of aerenchyma tissue, which is assumed to help aerate the underground root systems (Crisp *et al*., 1990; Tomlinson, 1986).

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Growing in waterlogged conditions, with tidal flows, also poses problems for seedling establishment. A number of different strategies are exhibited by the seeds of mangal species. The most common feature of seaward species is vivipary. Here the seed typically germinates on the plant, producing a long tapered and fleshy root. Initial growth rates are also strong, with the early establishment of an extensive root system. Species from more landward situations often have corky or rounded fruits which appear to withstand prolonged immersion, and are able to float considerable distances. While the development of dartlike seedlings from vivipary would suggest a mechanism for survival, Tomlinson (1986) notes a range of sources which discount this. Indeed, the value to the plant of the precociously germinated seedling may be more related to a dispersal mechanism (Crisp *et al*., 1990).

Physiological mechanisms to combat hypersaline conditions are widespread through mangal species. Three Australian genera (*Avicennia*, *Aegialitis* and *Aegiceras*), all frequently found in hypersaline situations, possess salt secreting glands which help in the general process of excluding and excreting salt. All genera have physiological mechanisms to exclude salt intake, in common with most halophytes. Salt secretors, however, have the extra mechanism of maintaining relatively high salt concentrations in their xylem. The salt is secreted as sodium chloride crystals from specially modified salt glands at the edges and apex of the leaves.

Diversity and distribution

Mangrove species come from rather few families. Many of the more 'typical' species are from the Rhizophoraceae. Other families with a number of species, or key species, are Sonneratiaceae, Combretaceae, Bombacaceae, Verbenaceae, Myrsinaceae, Myrtaceae, Acanthaceae, Meliaceae and Malvaceae. Key genera in the Australian mangal are, in declining order of significance, *Avicennia*, *Rhizophora*, *Aegiceras*, *Ceriops*, *Bruguiera*, *Sonneratia*, *Excoecaria*, *Camptostemon*, *Xylocarpus*, and *Heritiera* (see Bunt *et al*., 1982; Bridgewater, 1989).

The last three genera contain the tallest tree mangroves in Australia, reaching their best in Queensland. *Heritiera* and *Bruguiera* are also found as tall trees on the elevated limestone terraces of Christmas Island in the Indian Ocean (Du Puy, 1993). Although not directly marine, this situation provides a fascinating example of how species which are typically marine can adapt. Beard (1967) notes an example in Western Australia of *Avicennia* growing over 40 km inland from the coast, and there are many examples around the coastline of *Avicennia* growing in apparently dry dunes. The local hydrography may provide an answer here, with underground marine inflow, or brackish outflow, providing the conditions normally experienced at the land-sea interface.

Present-day global distribution of mangal and its component species suggests that the Indo-Malayan region was the focus for mangrove evolution. Fossilised pollen and wood from south-western Australia (Churchill, 1973) indicates that some genera (*Nypa*, *Sonneratia*, *Avicennia*) were present in the mid-Eocene. The mangrove flora of this region today has only one species (*Avicennia*), indicating changes in climate and water temperature, but this evidence, coupled with further fossil data showing continuous mangrove vegetation from the lower Tertiary in Sulawesi, suggests a possible origin of mangrove flora and mangrove habit in the Australian region.

Despite this, the current suite of mangrove species in Australia contains only one endemic, *Avicennia integra* (Duke, 1988), which appears restricted to northern Australia, although some species are regionally restricted (*Osbornia octodonta*, *Aegialitis annulata* and *Bruguiera exaristata*). Biogeographic analyses of the mangal have largely been cursory. A significant analysis of the Western Australian coastline was made by Semeniuk *et al.* (1978). These data were re-presented, with data for the eastern states, by Hutchings & Saenger (1987). A more detailed analysis was made for southern and western Australia by Bridgewater (1989). A re-interpretation of available data for Australia is made for this volume, and appears as Fig. 89.

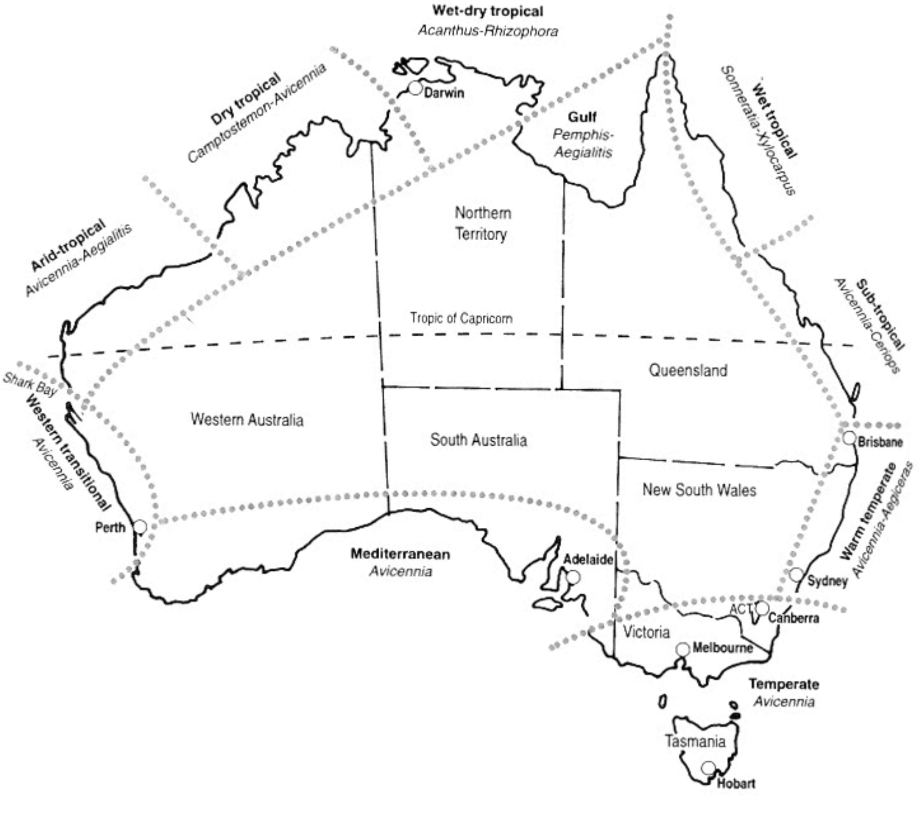

Figure 89. Biogeographic regions of mangroves in Australia. The divisions are a combination of climatic conditions and major or significant mangrove genera. In Western Australia a transitional area occurs with little mangal development except at Shark Bay. There the presence of halophytes typical of both the arid tropical and mediterranean regions suggests a transitional nature to this zone.

Ecology

Why is mangal important ecologically? Like saltmarshes, mangrove forests are important buffers between land and sea – highly dynamic systems that can change extent and composition over quite short periods, and show quite marked changes over decades (Bird & Barson, 1975; Crisp *et al*., 1990).

Zann (1995) notes that Australia has the third largest area of mangal for any one country in the world. Only Brazil and Indonesia have larger areas. Australia also has the unusual feature of coastlines where mangrove and salt-marsh merge in both a Mediterranean climate (Bridgewater & Cresswell,1993) and Temperate climate (Bridgewater, 1982a, 1982b).

Zann (1995) also stresses the important ecological role that mangroves play: 'providing habitats and nurseries for many fish, [they] form a buffer for estuaries from sediments and for coastlines from storm waves, are natural nutrient filters, and are critical habitats for many birds and other wildlife'. Such views are echoed by Hutchings & Saenger (1987).

Most mangrove species are tall trees and shrubs, and are home to many vertebrate species. These include 13 species of birds (although up to 250 species are thought to associate with or visit mangal systems), fruit bats (*Pteropus* spp), crocodiles, skinks, sea snakes, other snakes (including the venomous black-bellied swamp snake) and around 150 species of fishes. The invertebrate fauna is even more diverse, although mainly dwelling in the sediments (Clough *et al.*, 1982).

Some species (e.g. *Sonneratia alba*) grow where the tide covers the lower third of their stems daily. Other species (e.g. *Ceriops tagal*) are found growing in hypersaline conditions, with irregular tidal inundation. Yet others (e.g. *Xylocarpus granatum*) are found only where freshwater flows are sufficiently strong to significantly reduce the salinity of the seawater. For those authors who adopt a wide view of mangal, the range of habitats is much wider, including those of chenopods and even salt-tolerant grasses which occur with shrubs along the northern and western coastlines.

The mangal is a complex series of plant communities, often defined by only a few species. Communities are graded or zoned on the shoreline depending on the local coastal geology, hydrology and climate. Australia has the most southerly occurrence of a mangrove species, near Corner Inlet, in southern Victoria. There, fully fertile individuals of *Avicennia marina* between 0.5 and 0.75 m in height occur. This population represents the highest latitude reached by mangrove species in either Hemisphere. Around the southern coast of Victoria, South Australia and Western Australia extensive mangal occurs in suitable estuaries. This community is monospecific: *Avicennia marina* occurs as a shrub or tree to 2–3 m in height. Landward saltmarshes frequently occur, dominated by such species as *Sarcocornia quinqueflora*, *Suaeda australis* and *Samolus repens*. These communities are widespread in the region of Australia typified by a Mediterranean climate type (Bridgewater, 1982b).

On the western coastline of Australia mangal is relatively scarce, occurring in suitable habitats as a thin band between the sea and the highly arid interior. On the east coast of the continent mangal is more frequent, with species richness increasing towards lower latitudes.

The most extensive and biodiverse areas of mangal occur along the northern coastline of Australia, from the Gulf Country of Queensland to the Kimberley region of Western Australia. This is also the most richly textured mangal landscapes. In terms of diversity, the 25–26°S region is a major point of change in Australia. Northwards, the mangal is more species-rich, whatever the climate (see Bunt *et al*., 1982; Wightman, 1989). While not as diverse as that of the north coast, the tallest mangal is to be found along the east coast of Cape York Peninsula, north of Cairns.

Threats and conservation

Australia has had a relatively good record of conservation of mangal, surpassing that of many other countries. This is partly due to lower population densities in Australia, but more importantly, because much of the Australian mangal is in isolated areas. Unlike many other countries with substantial mangrove areas, Australia has no traditional human occupation and use of such areas, and little development of aquaculture facilities. However, mangal is now threatened by many human activities, particularly the filling and draining of coastal wetland systems, and the development of port and marina infrastructure.

The most affected mangal is that south of 32°S, where industrial and residential development have taken their toll. There is also a threat from the introduced grass, *Spartina* × *townsendii*, which was originally introduced to control silting in estuaries, but now has the potential to damage stands of mangal in Victoria (Rash *et al.*, 1996).

While other vegetation types, particularly other wetlands, have suffered degradation and species extinction in the last 200 years, it appears unlikely that any species of mangrove, or species associated with mangal, has become extinct in Australia, or is especially endangered. It is interesting that Aboriginal Australians appear to have relatively few uses for mangroves, in contrast to other indigenous cultures in the region. For the future, careful management and monitoring of remaining mangal and its hinterland will be critical to ensuring a relatively intact community remains.

THE MARINE ANGIOSPERMS

Diana I. Walker[1]

The Australian marine environment occupies some 11 million km^2, stretching from the 50 000 km of coastline outwards for a distance of 200 km (the Australian Exclusive Economic Zone), to depths of thousands of metres. Much of this environment is, however, unsuitable for photosynthetic organisms, which rely on sufficient light being available to support net photosynthesis (Kirk, 1994). The surface layers of the oceans are occupied by phytoplankton (micro-algae), but this is a very thin layer (tens of metres) relative to the depth of waters off the continental shelf (Price, 1990). The shallow waters along coastlines where land and sea meet are the most productive and diverse environment for marine macrophytes (Mann, 1982), both seaweeds (algae) which occur mainly on rocky shores, and seagrasses (marine angiosperms) found mainly on soft sandy or muddy bottoms. This section focuses on the marine angiosperms in Australian waters.

The seagrasses are a specialised group of only 58 species which evolved from terrestrial angiosperms about 100 Mya (den Hartog, 1970; Waycott & Les, 1996). The lack of species diversity and the antiquity of species suggest an extremely slow rate of evolution within the group (den Hartog, 1970; Les, 1988; Larkum & den Hartog, 1989). Terrestrial angiosperms had evolved mechanisms to cope with life on land, developing adaptations such as thick cuticles to prevent water loss, stomata for gas exchange, support tissues and conducting vessels (Raven, 1985). In recolonising maritime habitats seagrasses needed to develop mechanisms to cope once more with a submerged aquatic existence, in particular, tolerance of a saline medium while submerged completely, an anchoring mechanism, and underwater pollination (Arber, 1920).

Seagrasses have creeping rhizomes with roots (Tomlinson, 1982) that anchor the plants in the sediment in a turbulent environment. This rhizome bears upright shoots which can be ribbon-like (e.g. *Posidonia*) or with lignified erect shoots with terminal leaf clusters (e.g. *Amphibolis*). They do not possess stomata and have only a very thin cuticle (Kuo, 1983) which facilitates gas exchange. Seagrasses have unusual floral structures and both pollen and stigmas show adaptations to their saline medium (McConchie, Ducker & Knox, 1982; McConchie, Knox, Ducker & Pettitt, 1982). Approximately 75% of seagrasses are dioecious, having separate male and female plants (den Hartog, 1970; Pettitt *et al.*, 1981; Les, 1988; Cox & Humphries, 1993) compared to only 4% of angiosperms as a whole (Richards, 1986).

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Seagrasses have their greatest species richness in Australia, where there are also some of the largest meadows (Walker & Prince, 1987). This chapter explores this richness and distribution. The ecological significance of seagrasses are described, as well as the large scale losses that have resulted from human activities.

Diversity and distribution

The Australian coastline has 30 of the 58 species of seagrass that occur worldwide (Table 28) (Kuo & McComb, 1989) (Figs 123, 124). These come from 11 of the 12 worldwide genera, and all four families (Hydrocharitaceae, Posidoniaceae, Cymodoceaceae, Zosteraceae) from two orders (Hydrocharitales and Najadales) (Tomlinson, 1982). These species occur in shallow, relatively clear water around Australia, from tropical to cool-temperate waters.

The distributions of seagrass species (Table 28) fall into two main types. Sixteen species are endemic to Australia, and confined mainly to temperate southern Australian. Two other temperate species of Zosteraceae are more widespread, one occurring only in Australia and New Zealand, the other only in Australia and Chile. A further 12 species are tropical, and found throughout the Indian Ocean and tropical Pacific region. These distributions reflect the length and diversity of Australian coastal habitats and the comparative isolation of the Australian temperate zone. The pattern of circulation of water around Australia (Fig. 90) reveals some of the potential links to the Indo-West Pacific Region (Jeffrey *et al.*, 1990).

In tropical areas of Australia, seagrasses often occur as mixed assemblages (Poiner *et al.*, 1989) with biomass values of c. 200 g/m^2 and very rapid rates of turnover (Brouns, 1984, 1985, 1987a, 1987b; Brouns & Heijs, 1986). These seagrasses are often associated with coral reef environments where they occur in the shelter of lagoons, although they are also found in embayments such as in the Gulf of Carpentaria (Poiner *et al.*, 1989). They are important as food for dugongs and turtles (Lanyon *et al.*, 1989)

In southern Australia, particularly Western Australia and South Australia, there are large, mainly monospecific meadows of southern Australian endemic species. These meadows have high biomasses (500–1000 gC/m^2) and high productivities (>1000 gC/m^2/yr^1) (Hillman *et al.*, 1989). Southern Australian seagrasses are unusual in that they occur in water bodies exposed to levels of water movement only slightly reduced from open ocean environments (Walker & McComb, 1992). Where seagrasses occur elsewhere in the world they are confined to protected water bodies such as estuaries and lagoons. Australian species do require some protection and most seagrasses occur in habitats with extensive shallow sedimentary environments, sheltered from oceanic swells, such as embayments (e.g. Shark Bay and Cockburn Sound, Western Australia; Spencer Gulf, South Australia; Westernport Bay, Victoria), protected bays (e.g. Botany Bay, New South Wales; Jervis Bay, Australian Capital Territory; Geographe Bay and Frenchman's Bay, Western Australia) and lagoons enclosed by fringing reefs, both tropical (associated with coral reef environments) and temperate (e.g. the Western Australian west coast from Bunbury to Kalbarri) (see Larkum *et al.*, 1989, for full descriptions).

Table 28. List of species of marine angiosperms reported from Australia, with their biogeographic distribution (adapted from Kuo & McComb, 1989).

Species	Distribution
HYDROCHARITACEAE	
Enhalus acoroides (L.f.) Royle	Indo-West Pacific
Halophila decipiens Ostenf.	Indo-West Pacific, Caribbean
Halophila minor (Zoll.) Hartog	Indo-West Pacific
Halophila ovalis (R.Br.) Hook.f.	Indo-West Pacific
Halophila spinulosa (R.Br.) Asch.	Indo-West Pacific
Halophila australis Doty & Stone	Australian endemic
Halophila tricostata Greenway	Queensland endemic
Thalassia hemprichii (Ehrenb.) Asch.	Indo-West Pacific
POSIDONIACEAE	
Posidonia australis Hook.f.	Southern Australian endemic
Posidonia angustifolia Cambridge & Kuo	Southern Australian endemic
Posidonia denhartogii Kuo & Cambridge	Southern Australian endemic
Posidonia sinuosa Cambridge & Kuo	Southern Australian endemic
Posidonia coriacea Cambridge & Kuo	Western Australian endemic
Posidonia kirkmanii Kuo & Cambridge	Western Australian endemic
Posidonia ostenfeldii Hartog	Western Australian endemic
Posidonia robertsoniae Kuo & Cambridge	Western Australian endemic
CYMODOCEACEAE	
Amphibolis antarctica (Labill.) Sond. & Asch. ex Asch.	Southern Australian endemic
Amphibolis griffithii (J.M.Black) Hartog	Southern Australian endemic
Cymodocea angustata Ostenf.	Tropical Western Australian endemic
Cymodocea rotundata Ehrenb. & Hempr. ex Asch	Indo-West Pacific
Cymodocea serrulata (R.Br.) Asch. & Magnus	Indo-West Pacific
Halodule pinifolia (Miki) Hartog	Indo-West Pacific
Halodule uninervis (Forsk.) Asch.	Indo-West Pacific
Syringodium isoetifolium (Asch.) Dandy	Indo-West Pacific
Thalassodendron ciliatum (Forssk.) Hartog	Indo-West Pacific
Thalassodendron pachyrhizum Hartog	Western Australian endemic
ZOSTERACEAE	
Heterozostera tasmanica (Asch.) Hartog	Southern Australia, Chile
Zostera capricorni Asch.	Australia, New Zealand
Zostera mucronata Hartog	Southern Australian endemic
Zostera muelleri Irmisch & Asch.	Southern Australian endemic

The suitability of habitats on the south-western Australian coast for seagrasses has been attributed to these protected lagoonal systems and to water temperature (Kirkman & Walker, 1989). Kirkman & Kuo (1990) describe the processes affecting these communities.

South-western Australia in particular has the highest diversity of *Posidonia*, with seven of its eight species occurring in this region (Cambridge & Kuo, 1979; Kuo & Cambridge, 1984). The only non-Australian species of *Posidonia* (*P. oceanica)* occurs in the Mediterranean. This speciation seems related to the more exposed nature of this part of the coast where the five members of the more leathery *P. ostenfeldii*-group are found (Kuo & Cambridge, 1984).

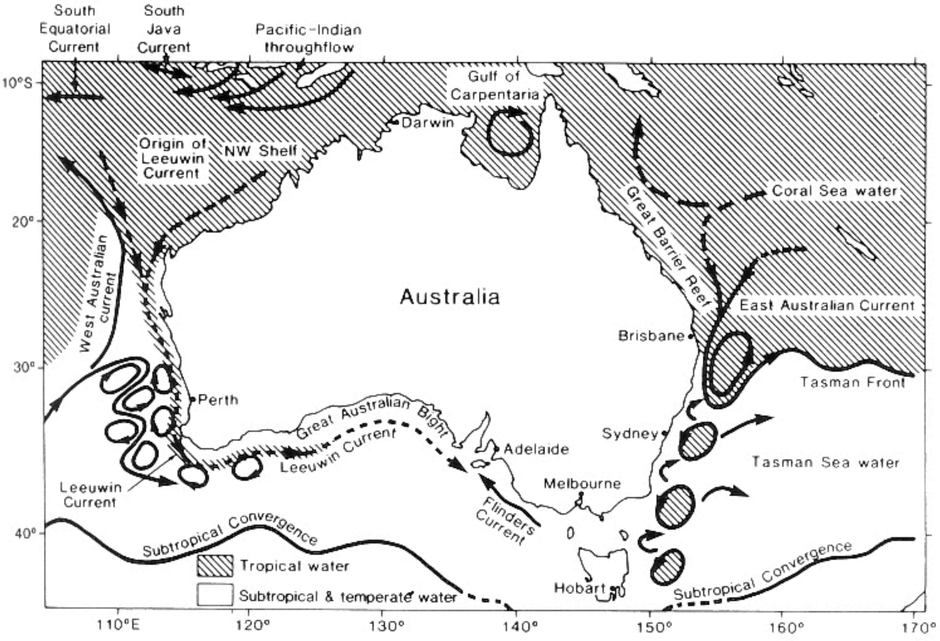

Figure 90. Australia's ocean circulation patterns (adapted from Jeffrey *et al*., 1990).

Ecological importance

Seagrasses provide a stabilising third dimension in an otherwise unstable environment. They are capable of colonising areas unavailable to macroalgae, most of which require a hard substratum for attachment. The presence of seagrasses changes the seabed from a two-dimensional structure of unconsolidated sediment into a complex three-dimensional structure incorporating the leaves, stems, rhizomes and roots of the seagrass themselves, plus extensive populations of epiphytic algae and invertebrate fauna. Many of the functional roles that seagrasses play depend on this three-dimensional structure.

Seagrasses lack the variety in habit that characterises terrestrial vegetation. Most seagrasses have long strap-like leaves, therefore biomass and leaf area are useful measures of complexity at small scales. The obvious exceptions to this are genera such as *Amphibolis* and *Thalassodendron*, with perennial woody stems, clusters of leaves, and large epiphytic algae growing on the stems.

Physical attributes

Water flow within a seagrass canopy encounters frictional resistance, therefore the current velocity drops (Fonseca & Fisher, 1986; Fonseca & Cahalan, 1992). As current velocity drops, the particle-carrying capacity of the water also decreases, which results in the deposition of fine particles within the meadow. Calcium carbonate, from epiphytic coralline algae (Walker & Woelkerling, 1988) and invertebrates such as molluscs (Hutchings *et al.*, 1991), and organic material produced within the seagrass meadow are also trapped (Walker & McComb, 1985). Furthermore, velocity-reduction by the canopy, in combination with the binding properties of the seagrass root and rhizome system, acts to stabilise the sediments. The net effect of seagrass meadows on sedimentation processes may be summarised as: less sediment erosion; increased sedimentation rates; a higher proportion of fine particle sizes and changes in the levels of organic matter and calcium carbonate. However, under conditions of orbital swell, as occur on much of the southern Australian coast, this increased sedimentation may not occur due to the more extreme physical environments (Walker *et al.*, 1996).

Chemical attributes

Compared to unvegetated areas, seagrass meadows represent considerable accumulations of carbon, nitrogen and phosphorus, particularly in the nutrient-poor environments they typically occupy (Hillman *et al.*, 1989; Fourqurean *et al.*, 1992). To maintain their high growth rates seagrasses also need large amounts of nutrients (nitrogen and phosphorus), and their requirements are met partly by uptake of nutrients from the sediments by the roots and rhizomes, and partly by uptake by the leaves from the water column (Hemminga *et al.*, 1991). It has been suggested that most seagrass nutrients are derived from the (largely bacterial) recycling of organic material within the meadows plus efficient internal recycling of nutrients: nutrients are withdrawn from senescing plant material before it is shed (Dennison *et al.*, 1987; Caffrey & Kemp, 1990; Yamamuro *et al.*, 1993; Erftemeijer & Herman, 1994). Bacterial populations both in the water column and in sediments associated with seagrass meadows are far higher than in unvegetated areas, and bacteria also occur as epiphytes on seagrass leaves (Moriarty & Boon, 1989). The growth of these microbial populations is supported by the organic carbon compounds that are exuded from live seagrass material and those released from the breakdown of the organic matter accumulating in seagrass meadows (Moriarty & Boon, 1989; Blum & Mills, 1991).

Biological attributes

Seagrasses are an important source of primary productivity on sandy substrata. Most research on seagrass ecology in Australia has been carried out on the large temperate genera *Posidonia* (Cambridge, 1975; Larkum, 1976; Kirkman & Reid, 1979; Kirkman *et al.*, 1979; Cambridge *et al.*, 1986; Silberstein *et al.*, 1986; Larkum & West, 1990; West, 1990) and *Amphibolis* (Walker, 1985; Walker & McComb, 1988, 1990; Walker & Cambridge, 1995), although a recent monograph has been published on *Halophila ovalis* (Hillman *et al.*, 1995). *Zostera capricorni* has also been the subject of detailed studies (Kirkman *et al.*, 1982; Larkum *et al.*, 1984; Abal *et al.*, 1994).

Algae epiphytic on seagrasses also contribute substantially to productivity. Cambridge (1975) and Silberstein *et al.* (1986) have documented algae on *Posidonia australis* and *P. sinuosa*, while epiphytes on *Amphibolis* have been studied extensively (Kendrick *et al.*, 1988; Borowitzka & Lethbridge, 1989; Borowitzka *et al.*, 1990). These epiphytes are more easily broken down and form a more palatable food source than seagrass tissue which is very fibrous.

Many invertebrate animals are found in association with seagrasses. Often these animals use the leaf canopy only for shelter, and only consume epiphytic algae. It is often suggested that seagrass meadows form a 'nursery' for juvenile invertebrates and fishes, a refuge from predation. The refuge value and the amount of habitat available to the fauna inhabiting seagrasses are frequently correlated with the 'complexity' of the habitat, as measured by plant biomass and/or plant surface area (Stoner, 1983; Virnstein & Howard, 1987a, 1987b; Ansari *et al.*, 1991; Mellors & Marsh, 1993; James & Heck, 1994).

Relationships between the abundance of plants and animals remain more or less constant for different species of seagrass and for different sites within the same general area (e.g. Virnstein & Howard, 1987a, 1987b; Howard *et al.*, 1989). Faunal assemblages rarely associate with particular seagrass species; rather they respond to a large number of environmental factors that differ between sites. Thus many animal species are common to adjacent beds of different seagrass species, but the fauna of a bed of any particular species of seagrass may be quite different to that of the same species growing elsewhere. This has been demonstrated in Western Australia for the invertebrate fauna of both subtropical seagrass meadows (Edgar, 1990; Edgar & Robertson, 1992) and temperate seagrass meadows (Hutchings *et al.*, 1991). Australian studies in temperate and tropical seagrass meadows have also demonstrated strong relationships between faunal abundance and the density of seagrass leaves, as measured by biomass (Howard *et al.*, 1989; Humphries *et al.*, 1992; Mellors & Marsh, 1993).

Fish diversity in and near seagrass beds varies enormously with depth, spatially, and with seagrass species (Ferrell *et al.*, 1993; Blaber *et al.*, 1995). Bare sand has been found to have fewer species of fish, (Bell & Pollard, 1989; Connolly, 1994), with only one or two species (as opposed to 39 in seagrass). Fish population density is also lower (Burchmore *et al.*, 1984).

Seagrasses provide foraging grounds for the largest single-species fishery in Australia, that of the Western Rock Lobster (*Panulirus cygnus* George). The catch has an annual value of about $A200 million and is largely taken between latitudes 28–32°S on the west coast (Phillips *et al.*, 1991).

Seagrass loss

The decline of seagrass meadows is a world-wide phenomenon (Walker & McComb, 1992). This may result from natural events such as 'wasting disease' (den Hartog, 1987) or high energy storms (Patriquin, 1975), but most seagrass loss has resulted from human activities, such as nutrient enrichment leading to eutrophication (Orth & Moore, 1983; Bulthuis, 1983; Cambridge & McComb, 1984; Neverauskas, 1987), or land reclamation and changes in land use (Kemp *et al.*, 1983). These studies have documented changes in ecology and some ecosystem processes, but there is still a need for greater understanding of these processes, in order to manage these ecosystems effectively.

The major man-induced declines of seagrass in Australia and their suggested causes are summarised by Walker & McComb (1992). They are discussed in more detail by Shepherd *et al.* (1989). Although many factors may interact, most cases of seagrass decline have resulted from a decrease in light reaching seagrass chloroplasts, hence reducing net effective seagrass photosynthesis. This may result from increased turbidity from living or non-living particulates in the water, increased shading by the deposition of silt or from the growth of epiphytes on leaf surfaces or stems. Seagrass meadows occur between an upper limit imposed by exposure to desiccation or wave energy, and a lower limit imposed by penetration of light at an intensity which allows net photosynthesis. A small reduction in light penetration through the water results in elimination of seagrass at the lower edge of a meadow, while particulates on leaves reduce meadows over extensive areas of shallower water.

The turbidity of the water column above seagrasses can increase through discharge or resuspension of fine material in the water column (e.g. sludge dumping, dredging). Increased nutrient concentrations, from discharge of sewage and industrial wastes, or agricultural activity in catchments, may stimulate phytoplankton growth, significantly reducing light penetration through the water column (Chiffings & McComb, 1981; Lukatelich & McComb, 1986).

Nutrient enrichment can also result in greater growth of macroscopic and microscopic epiphytic algae on leaf surfaces. Macroalgae dominate over seagrasses under conditions of marked eutrophication. This effect is due to the growth of epiphytes (both microscopic and macroscopic), and associated loose-lying species (e.g. *Ulva*, *Cladophora*, *Enteromorpha*, *Ectocarpus*) which may originate as attached epiphytes. The effect of such epiphytes on the health of seagrass beds has been demonstrated in Cockburn Sound, Western Australia (Cambridge & McComb 1984, Silberstein *et al.*, 1986).

Physical removal of seagrass is also a major threat. Boat moorings around Australia can cause localised damage (Walker *et al.*, 1989). Harbour and groyne construction, which change the wave energy regime, can also affect seagrass growth. Increased wave or current energy may increase sedimentary erosion and lead to fragmentation of seagrass beds and loss of the rhizome mat. The dredging of Botany Bay, New South Wales, appears to have precipitated this effect in the *Posidonia* beds there (Larkum & West, 1990). If the wave energy regime is decreased by man-made structures then increased deposition of sediment is probable (Harrison, 1987).

Conservation value

Australia's seagrass beds have the world's greatest species richness with a high level of endemism, as well as being some of the most extensive (Walker & Prince, 1987). In addition, they support rich communities of algae, invertebrates and vertebrates. These communities rely on the stable three-dimensional structure of the seagrass canopy. Seagrass beds thus provide a large contribution to biodiversity on sandy bottoms. Their vulnerability to development pressures on Australia's coastal environment means that effective management will be needed if Australia is to retain these rich plant communities.

Acknowledgments

The contributions to our understanding of seagrasses and their biology by Professor A.J.McComb and Associate Professor John Kuo are gratefully acknowledged. D.I.Walker is grateful to Karen Hillman for discussions on the ecological significance of seagrasses.

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UTILISATION OF THE AUSTRALIAN FLORA

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The Australian vascular flora, with in excess of 20 000 species, a very high proportion of which are endemic, would be expected to yield a large number of useful products. Certainly, before 1770 the Aboriginal inhabitants used a large number of plants for food, tools, weapons and remedies, and many still do. Yet with colonisation by Europeans, and the development of large scale farming and horticulture, little use was made of the native flora, with the exception of timber. Until very recently, the only Australian species grown extensively for food were *Macadamia integrifolia* and *M. tetraphylla*, and even here, the first major plantations were developed in Hawai'i, not Australia (O'Neill, 1996).

A number of accounts of useful plants were written in the 19th century, although most concentrated on plants of use to industry, particularly timber and related products. One of the most comprehensive references from this period, and one which discussed a number of indigenous as well as industrial uses for plants, was Maiden (1889).

Belatedly, the potential of the Australian flora to provide useful products has been recognised. A number of recent books give an overview of useful native plants (e.g. Cribb & Cribb, 1982; Bindon, 1996), while others deal with particular subjects, particularly bush foods. This chapter surveys some of the more important of these products, without pretending to be comprehensive. Some large industries such as ecotourism and bushwalking, built substantially but not entirely on the native flora and vegetation, are beyond the scope of this account, but cannot be discounted in any account of the contribution of the native flora to Australia's economic activity.

Aboriginal use of native plants

The indigenous inhabitants of Australia used many hundreds of native plants for food, shelter, weapons, implements, medicines, stimulants, adornment, fibre, rope, canoes and much more. Numerous books have been written on this subject, particularly in the last decade or two. While some traditional knowledge of the properties of the native flora has undoubtedly been lost, a surprising amount has survived. Documentation of traditional usage is gathering pace, with traditional peoples recording knowledge of their traditional plants, and others providing cross-cultural surveys of the amazing numbers of plants that have been used, and the diverse uses to which they have been put.

No attempt will be made here to try to provide a comprehensive account of this subject. A few subjects, such as food plants and medicinal plants will be discussed in some detail below, but for other uses only a selection of source materials can be quoted.

General books on indigenous use of plants include Bindon (1996), Cribb & Cribb (1982) and Isaacs (1987, 1996). More regional guides include Edgar *et al.* (1987), Goddard & Kalotas (1988), Latz (1995), Levitt (1981), Roberts *et al.* (1995), Smith (1991), Smith *et al.* (1993), Smith & Wightman (1990), Symons & Symons (1994), Turner & Henderson (1994), Wightman *et al.* (1991), Wightman *et al.* (1994), Wightman, Dixon *et al.* (1992), Wightman, Roberts & Williams (1992), Wightman & Smith (1989) and Zola & Gott (1992).

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Bush foods

The last decades of the 20th century have seen a growing interest in the native flora (and fauna) as a source of new and exotic foods. To a large extent this was triggered by a very successful television program *Bush Tucker Man*, narrated by Les Hiddins and screened by the Australian Broadcasting Commission in the late 1980s, although a specialist literature had been quietly building for some years (e.g. Cribb & Cribb, 1975; Jones, 1985; Low, 1988, 1989, 1991).

Until the 1990s only one commercial crop, macadamia nuts, had been developed from Australian native plants. This crop is discussed in more detail below. A few other species were used as minor food sources on a regional basis and almost entirely wild-collected. These included Quandong (*Santalum acuminatum*), Bunya nuts (*Araucaria bidwillii*) and Native Rosella (*Hibiscus heterophyllus*) (Keena, 1997).

Increasing interest in bush foods has led to the development of an incipient plantation industry to supplement wild collection. This supports a rapidly increasing boutique restaurant industry based on bush foods, either alone or as condiments for more traditional dishes. A specialist literature is quickly developing. A dedicated bi-monthly magazine, *Australian Bushfoods Magazine* was established in March 1997 to service both the grower and consumer markets. Books on growing, processing and cooking native food plants are appearing (e.g. Bruneteau, 1996; Cherikoff & Isaacs, 1989; Robins, 1996). Industry organisations such as the Australian National Bushfoods Industry Committee are being formed, and industry reports are beginning to appear. One of these reports (Graham & Hart, 1997) identified and discussed 15 taxa with particular potential for cultivation and development. These were *Acacia* spp. (Wattleseed), *Acronychia acidula* (Lemon Aspen), *Backhousia citriodora* (Lemon Myrtle), *Davidsonia pruriens* (Davidson Plum), *Eremocitrus glauca* (Wild Lime), *Hibiscus heterophyllus* (Wild Rosella), *Kunzea pomifera* (Muntries), *Podocarpus elatus* (Illawarra Plum), *Prostanthera rotundifolia* (Native Mint), *Santalum acuminatum* (Quandong), *Solanum centrale* (Bush Tomato), *Syzygium luehmannii* (Riberry), *Tasmannia lanceolata* (Native Mountain Pepper), *Terminalia ferdinandiana* (Kakadu Plum) and *Tetragonia tetragonioides* (Warrigal Greens). Phelps (1997) produced another report, on the bush foods industry in western Queensland. Geno (1997) provided an overview of bushfood organisations. A brief review of current CSIRO research on bush foods is given by Boland (1997), and research on *Acacia* was described by Morse (1997).

Articles on individual bush foods are numerous. The following are only a sample: *Acacia* (Gott, 1997; House & Harwood, 1992; B.King, 1997; Morse, 1997; Orr & Hiddins, 1992), *Araucaria* (J.R.King, 1997), *Backhousia* (Costin, 1997; Lake, 1998b), *Eremocitrus* (Phelps & Phelps, 1997; Sykes, 1997), *Kunzea* (B.King, 1998), *Microcitrus* (Birmingham, 1997; Sykes, 1997), *Santalum* (CSIRO Plant Industry Horticulture Industry, 1998; Fox, 1998; Matthews, 1997) *Solanum* (Cherikoff, 1998; Latz, 1998), *Syzygium* (Keena, 1998; Ringer, 1997), *Tasmannia* (Padbury, 1998). Note that *Eremocitrus* and *Microcitrus* are now often included in *Citrus*.

As well as literature on the bush foods industry, there is a growing literature on traditional use of native food plants. Recent books and articles include Bindon (1996), Brock (1993), Gott (1985), Latz (1995), Plomley & Cameron (1993), Roberts *et al.* (1995), Smith & Jumbun experts (1991), Stewart & Percival (1997), Zola & Gott (1992).

A number of studies have been made on the nutritional qualities of bush foods. A symposium in 1976 (Hetzel & Frith, 1978) discussed Aboriginal nutrition in Central Australia, including the food value of various native plant species. In 1984 a colloquium was held to discuss the food potential of seeds of Australian native plants (Jones, 1985). This workshop considered, among others, the food value of seeds of *Santalum* (Rivett *et al.*, 1985), *Erythrina*, *Canavalia* and other Fabaceae (Jermyn, 1985), *Acacia* (Kortt, 1985), *Athertonia* and *Elaeocarpus* (Irvine, 1985) and *Hovea* (Tucker *et al.*, 1985). A comprehensive summary of the nutritional qualities of over 500 foods (plant and animal) was presented by Miller *et al.* (1993). Devitt (1992) discussed the use of *Acacia* seeds as a traditional Aboriginal food, and Brand & Maggiore (1992) discussed the nutritional composition of a range of Australian *Acacia* seeds.

The farmgate equivalent gross value of the bush food industry was estimated at $10–12 million for 1995/96, and has about 200 'active participants' (Gare, 1997). The Australian Native Bushfood Industry Committee reported to a Senate inquiry (Woodley, 1998) that bushfood sales were $14 million in 1996, and expected to be $100 million by the year 2000. A modest amount of research funding is directed towards the industry: in 1997/98 the Rural Industries Research and Development Corporation (RIRDC) provided $82 000 in support of four projects on marketing and food safety for bush foods, and RIRDC is expecting to provide support of about $130 000 for similar projects in 1998/99 (RIRDC, 1998).

Macadamia

Macadamia integrifolia and *M. tetraphylla* are the source of macadamia nuts, an industry pioneered in Hawai'i (O'Neill, 1996), but now based on extensive plantations in South Africa, Zimbabwe, Malawi, Kenya, California, Central America, and, belatedly, in Australia, with smaller plantations elsewhere. Five other species produce inedible nuts with high levels of cyanide, and cyanide is produced even within germinating nuts and seedlings of the edible species (Dahler *et al.*, 1995; O'Neill, 1996). Doran & Turnbull (1997) provided silvicultural information for the two species yielding edible nuts.

Macadamia was introduced into Hawai'i experimentally in 1881 and 1892, but production expanded rapidly after widescale plantings of improved varieties in 1948. In Australia small plantings had been made by 1900, but it was not until 1965/66 that commercially viable areas were planted in this country. In the meantime many other countries had established plantations, and by 1987 world production amounted to 6 806 tonnes of kernels from 51 600 acres of plantations. Projections suggested that with new plantations coming on stream, production would rise to about 18 000 tonnes of kernel per annum within 5–10 years (Jodvalkis, 1987). At that time the market was dominated by Hawai'ian growers with 73% of world production. Australia had about 14%, but with extensive plantings coming into production, the projection was that, within 5–10 years, this would rise to about 20%. Nut production in 1987 is given in Table 29. The 1987 estimate of potential Australian production appears to have been pessimistic. O'Neill (1996) stated that Australian production had now exceeded that of Hawai'i, making Australia the leading world producer of macadamia nuts, and estimated that by the year 2000, some 2 million trees in northern New South Wales and southern Queensland would be coming into production, yielding crops worth more than $100 million annually.

Table 29. World macadamia nut production in 1987.
(Source: Jodvalkis, 1987).

Country	Acres	Bearing acres	1987 kernel production (tonnes)	Projected production, 5–10 years (tonnes)
Hawai'i	21 900	14 000	5000	9000
Australia	7100	2400	982	3570
South Africa	6200		240	1000
Kenya	2500		180	500
Malawi	1900		90	600
Costa Rica	5000	2000	180	2600
Guatemala	1000		134	180
Others*	6000			500
Totals	51 600		6806	17 950

*Brazil, Florida, Mexico, California, New Zealand, China

Wattleseed

Acacia seeds are a traditional Aboriginal food, particularly in Central Australia (Devitt, 1992), and have a high nutritional value (Brand & Maggiore, 1992; Miller *et al.*, 1993). Traditional methods of preparation were described by Orr & Hiddins (1987). Building on this tradition, the seeds of a number of Australian *Acacia* species are being investigated as a source of food for use in the growing bushfood industry (Gott, 1997; Harwood, 1994; House & Harwood, 1992; B.King, 1997; Maslin & McDonald, 1996; Maslin *et al.*, 1998; Morse, 1997).

Not all *Acacia* species yield edible seeds, and many are poisonous, or require special treatment to make them safe for consumption. Kortt (1985) described proteinase inhibitors in some *Acacia* seeds, while Maslin *et al.* (1988) surveyed a number of species for cyanogenesis.

For those seeds which are edible without requiring special treatment to eliminate toxicity, preparation involves grinding and sometimes roasting. The 'flour' is added to products such as bread and damper, pasta, biscuits, icecreams and drinks.

Acacia victoriae is currently the most important species in the wattleseed industry. Most seed is wild-collected, but experimental plantations have also been established (Maslin *et al.*, 1987). Considerable potential exists in a number of other species: Thomson (1992) discussed *A. colei*, *A. cowleana*, *A. tumida*, *A. adsurgens*, *A. oligophleba*, *A. coriacea* var. *pendula* and *A. glaucocaesia*; Maslin *et al.* (1998) listed *A. murrayan*a and *A. victoriae* as the most promising species, followed by *A. jennerae*, *A. microbotrya*, *A. pycnantha*, *A. retinodes*, *A. rivalis* and *A. saligna*. Criteria for economic seed production include: regular, heavy, synchronised seed production, relatively large seed size, habit of plant in relation to ease of harvest (including potential for coppicing), ease of establishment, and longevity (Maslin *et al.*, 1998).

Experimental *Acacia* plantations have been established abroad, particularly in the Sahel of Africa (Cossalter, 1987; Souvannavong & de Framond, 1992), to provide a source of firewood and seed for food.

Medicinal plants

As for bush foods, there is a very large literature on the use of Australian native plants for medicinal purposes. Indigenous peoples are known to have used very many different plants to treat illness, to relieve symptoms, and as stimulants. Many of these remedies have been recorded in the literature, but a large number still survive only in oral tradition, while others have undoubtedly been lost. The subject is too varied to be treated in detail here. Useful sources of information include Barr *et al.* (1988, 1993), Bindon (1996), Cribb & Cribb (1981), Henshall *et al.* (1980), Isaacs (1987), Kyriazis (n.d.), Lassak & McCarthy (1983), Latz (1995), Low (1990), Stewart & Percival (1997), Wightman *et al.* (1994) and Zola & Gott (1992).

From the early 1940s until the late 1970s CSIRO was involved in a major screening program of Australian native plants, searching for medically active chemicals. A major target was alkaloids, but triterpenes, diterpenes, phytoecdysteroids, flavanoids and phenolics were also extracted and studied. This Australian Phytochemical Survey was conducted largely under the direction of L.J.Webb and J.R.Price, but involved field botanists such as W.T.Jones, T.G.Hartley and many others. In 1958 the screening was extended to Papua New Guinean plants. The results of the screening were published by Collins *et al.* (1990). A literature survey, preliminary to the Australian Phytochemical Survey, was carried out by Webb (1948). Other surveys have been undertaken, many associated with cancer research. The most recent major bioprospecting survey is that organised by the Australian Medical Research and Development Corporation (AMRAD), using the resources of herbaria in Tasmania, Victoria and the Northern Territory (Anonymous, 1996).

A number of Australian native plants have been developed as crop plants for the drug industry. One of the best known is *Duboisia*. Two species, *D. myoporoides* and *D. leichhardtii*, are major sources of the alkaloids scopolamine (hyoscine) and hyoscamine, used for pupil-dilation in ophthalmology, to prevent air- and sea-sickness, and in the treatment of stomach ulcers. An industry based on wild-collected material began in a small way in the late 1800s, expanding rapidly in the 1940s. Plantations on a broad scale were not established until the late 1950s. By the 1980s plantations of selected forms had been established in the South Burnett area of Queensland (Cribb & Cribb, 1981; Ohlendorf, 1996).

Two Australian *Solanum* species, *S. aviculare* and *S. laciniatum*, have also been grown as plantation crops for the extraction of solasodine, a steroid used in the manufacture of contraceptive pills and other products. Major plantations were established in southern Russia and Hungary from about 1958 (Swan, 1975; Cribb & Cribb, 1981; Symon, 1994). Plantation trials in Australia in 1978–1981 and in New Zealand in 1964–1982 were unsuccessful (Symon, 1994).

Cribb & Cribb (1981) and Lassak & McCarthy (1983) describe a number of other plants of minor pharmaceutical importance.

A special category of medicinal plants are those yielding essential oils and other aromatic compounds. Low (1990) records that extracts from various plants, particularly *Melaleuca*, *Eremophila* and *Callitris*, have been used for thousands of years to treat respiratory complaints, sores, diarrhoea, headaches and chest pains, and as a mosquito repellent. In the last 200 years an extensive essential oils industry has developed, and this is discussed in more detail below.

Horticulture and floriculture

The flora of Australia created enormous interest in Europe in the late 18th century, once the novelty of the many new plants collected by Banks and Solander, and those who followed them, was revealed. Although illustrations of the Banks and Solander collections were not published until the twentieth century, many others found their way into the illustrated journals of the period.

Cavanagh (1990) has provided a detailed account of Australian plants cultivated in England between 1771 and 1800, beginning with seeds and plants sent back in the ships of the First Fleet in 1789. The flood of novelties from Australia and South Africa in particular, during this period, were a major stimulus to the establishment of important periodicals such as Curtis' *The Botanical Magazine* (1787–) and Andrews' *The Botanist's Repository* (1797–). By 1800 170 species (84 genera), mostly from the vicinity of Sydney, were in cultivation in the nursery trade in England. Nelson (1990) documented the trade, both within England, and to and from continental Europe, in the period to 1840, and the extensive literature that was developed to describe and illustrate these novel taxa.

Many of the earliest settlers made a sparse but steady living from sending dried specimens, seeds and plants back to the nurseries of England. One of the first was James Caley in New South Wales (Currey, 1966); another was James Drummond in Western Australia (Erickson, 1969).

Like all fashions, the fascination with Australian flora faded, and by 1840 Australian plants in Europe were largely confined to botanic gardens (Nelson, 1990). This fall from popularity may have been partly due in changes to heating methods in European hothouses. The introduction of steam heating systems increased humidity in hothouses and conservatories and most of the Australian plants died (Hamilton & Bruce, 1998). Their place was taken by tropical plants from South America and South East Asia. The decline in popularity had been foreshadowed even earlier, however. The first books and journals describing Australian plants had sold well, but by 1810, when Robert Brown produced the first part of a planned 2-volume account of the plants that he had discovered in Australia between 1801 and 1805

(Brown, 1810), sales were so poor that the book was withdrawn from sale and the second part never completed.

Within Australia the native flora attracted only a passing interest for the next 150 years. Conspicuous taxa such as *Eucalyptus*, *Acacia* and *Banksia* were adopted by local authors and artists to lend authenticity to their works. The Coolabah (*Eucalyptus microtheca*, syn. *E. coolabah*) gained fame from A.B. (Banjo) Paterson's *Waltzing Matilda*, wattle gained informal acceptance as the national flower (with *A. pycnantha* becoming the official floral emblem in 1988), and gumnuts (*Eucalyptus* spp.) and *Banksia* spp., along with a few others, received popular recognition in May Gibb's *Snugglepot and Cuddlepie* books of 1918–1921. However, with the exception of some botanic gardens, and limited street plantings, Australian flora was little grown or appreciated until the mid-20th century. Symptomatic of this disregard is an article on Australian stamp design (McQueen, 1988) which barely mentions flora. Hewson (this volume) discusses in more detail the portrayal of the native flora in art, craft and literature.

The 1960s brought an increased national awareness of the Australian flora, coupled with a heightened interest in the environment. One manifestation of this was the establishment of the Australian National Botanic Gardens in Canberra, dedicated to the growing and display of Australia's native flora. The first plantings were made in 1945, but it underwent its major development in the 1960s, and opened to the public in 1967. It now displays some 90 000 plants representing about 5000 species, a quarter of Australia's vascular flora.

In 1958 the Society for Growing Australian Plants was established, and by the 1970s was thriving. It had branches in all States, and specialist study groups for popular families and genera. It continues to prosper, and has its own journal, *Australian Plants*.

The Nursery Industry

Australian native plants surged in popularity as garden plants in the 1970s, on a wave of national pride, and the continuing increase in environmental awareness. Native species were seen to offer advantages in terms of lower water requirements, as well as having novelty value and being useful to attract native fauna to gardens.

Horticultural use has led to the development of an enormous literature on the growing of Australian native plants. Examples include general and regional works (e.g. Blombery & Maloney, 1994; Brock, 1993; Doran & Turnbull, 1997; Elliot & Jones, 1980–; Harris, 1977, 1980; Langkamp, 1987; Newbey, 1968; Wrigley & Fagg, 1996). Works on particular groups, families and genera include those on ferns (Duncan & Isaac, 1986; Goudey, 1988; Jones & Clemesha, 1981), palms (Jones, 1987), climbing plants (Jones & Gray, 1988), *Acacia* (Simmons, 1981, 1988; Tame, 1992), *Grevillea* (Wrigley & Fagg, 1989; Olde & Marriott, 1994–1995), *Banksia* (George, 1984a; Wrigley & Fagg, 1989), *Eucalyptus* (Holliday & Watton, 1980), *Melaleuca* and related genera (Wrigley & Fagg, 1993), Proteaceae (Blombery & Maloney, 1992; George, 1984b; Wrigley & Fagg, 1989), Asteraceae (Salkin *et al.*, 1995) and Orchidaceae (Jones, 1988; Lavarack & Gray, 1985; Sharp, 1970). Many more could be cited. In addition, several monthly gardening magazines with national circulation carry regular articles on growing native plants.

The Australian nursery industry was estimated to be worth about $1.8–2 billion in 1992/1993 (Swane, 1995). Unfortunately, no figures appear to be available on what proportion of this trade involves native plants. Casual observation suggests that a figure of 20% or more would be a good approximation. Swane saw a bright future for the nursery industry, with increasing use of native plants as ground cover and feature plants, in low-maintenance, low water use gardens.

The Cut Flower Trade

Following from the renewed interest in growing native plants was a greatly increased acceptance, and demand, for native flowers in floriculture, and this triggered development of a new industry, the Australian wildflower trade.

The earliest production for the cutflower industry came from wild harvesting of a limited range of species. In the eastern States wild harvesting of Waratah (*Telopea speciosissima*, *T. oreades*) was the main target, while in Western Australia, *Banksia* spp., *Dryandra* spp., *Verticordia* spp., *Podocarpus drouynianus* and *Stirlingia* spp. were extensively picked. For example, in Western Australia in 1980/81 over 6 million stems of these 5 genera were bush-harvested. By 1995 the number had risen to 13 million stems (*Agonis* had displaced *Dryandra* in the top five genera), although an increasing proportion of production was from 'managed bush blocks' (Karingal Consultants, 1997). The impact of wild harvesing on natural populations was examined by Woodley (1998).

Since the early 1980s Australian native cutflower production has increasingly come from plantations. As this new aspect of the floriculture industry developed, workshops and conferences were held to shape and standardise production. In 1982 a National Technical Workshop on Production and Marketing of Australian Wildflowers for Export and a seminar on Production and Marketing of Wildflowers were held in Perth (University Extension, University of WA, 1983), and in 1989 a conference on The Production and Marketing of Australian Flora was sponsored by the Western Australian Department of Agriculture and Australian Special Research Fund (Western Australian Department of Agriculture, 1989).

A survey of the Australian native cutflower industry was conducted by Karingal Consultants for the Rural Industries Research and Development Corporation in 1993 (Karingal Consultants, 1994), and repeated in 1996 (Karingal Consultants, 1997). The 1996 survey revealed a total of 1926 hectares of Australian wildflowers cultivated for the cutflower trade (this figure excludes South African genera such as *Protea*, *Serruria*, *Leucospermum* and *Leucadendron* which are commonly included in 'Australian wildflower' statistics). The industry involved 445 growers, employed about 1362 people, and the most important genera cultivated were *Chamaelaucium* (767 hectares), *Banksia* (319 hectares), *Thryptomene* (251 hectares), *Eucalyptus* (132 hectares), *Blandfordia* (69 hectares), *Anigozanthos* (87 hectares), *Verticordia* (39 hectares), *Agonis* (39 hectares), *Ixodia* (38 hectares), *Boronia* (24 hectares), *Stenanthemum* (23 hectares), *Dryandra* (22 hectares), *Leptospermum* (21 hectares), *Telopea* (16 hectares), *Melaleuca* (15 hectares) and *Ozothamnus* (14 hectares). This compares with 312 hectares of *Protea*, 199 hectares of *Leucodendron*, and 68 hectares of *Leucospermum*. In depth studies are now starting to appear on specific crops. Examples are those of Lewis *et al.* (1997) on Rice flower (*Ozothamnus diosmifolius*) and Slater (n.d.) on *Baeckea* and *Scholtzia*. These are supported by magazine articles such as those of L.Turnbull *et al.* (1997) and Warfield (1997) on *Ozothamnus* and *Cassinia*, Slater *et al*. (1997) on *Ozothamnus diosmifolius*, Gollnow (1997) on *Blandfordia grandiflora*, *Ceratopetalum gummiferum*, *Telopea speciosissima*, *Anigozanthos* and *Macropidium* and Konig (1998) on *Schoenia* and *Rhodanthe*.

Exports of fresh and dried/preserved Australian native cutflowers and foliage in 1996 were worth about $20–25 million, with the biggest markets being Japan, North America and the EEC (Karingal Consultants, 1997; Lewis *et al.*, 1997). The domestic market is approximately equal to the export market. It is estimated that the worldwide trade in Australian native flowers is worth $440 million annually (Hamilton & Bruce, 1998). Australia's share of this is thus only about 10%.

Forestry

Australia has about 41 million hectares of native forest, predominantly *Eucalyptus*. About 6.9 million hectares is available for wood production (Lacey *et al.* (1990). This resource has been exploited for timber production, wood chip for the paper and fibre board industry, for plywood, and for firewood. The forestry industry is a major employer: in Queensland alone in 1998 it employed 17 000 people and had a turnover in excess of $1.7 billion (Department of Primary Industry, Forestry, 1998). The establishment of a forest industry in New South Wales after 1788, and the subsequent development of the industry in that State, and of national training and management systems over the next 200 years was described by Grant (1989).

Traditionally, trees harvested for timber production have been removed from forests which are then allowed to regenerate, or have been harvested during the clearing of land for agriculture or other uses. From about 1910 however, commercial plantations of Californian *Pinus radiata*, established to provide the basis of a softwood industry, have led to replacement of native forests in some areas, and from the 1960s the commercial exploitation of native species for woodchips, principally for the paper industry, led to accelerating clear felling of forests. Concern at the rate of clearing and replacement led to a spirited debate (Routley & Routley, 1974; Woodgate & Black, 1988; Streeting & Hamilton, 1991; Dattner, 1993), which continues today.

In the 1990s the aim for Australia's native forests is sustainable management (McKinnell *et al.*, 1991). This still means different things to different people. To the forestry industry it means management of existing native forests for sustainable yield, supplemented by plantations (Florence, 1996). It means regeneration of forests *in situ* after clear felling, and selection of improved strains (Eldridge *et al.*, 1994). To conservationists, sustainable management means a phasing out of logging in native forests and replacement of the wild-harvested resource by plantation stock (Robins *et al.*, 1996). These concerns were addressed in the 1992 National Forest Policy Statement (NFPS) (Commonwealth of Australia, 1992), jointly developed by the Commonwealth, State and Territory Governments, in consultation with a wide range of individuals and organisations. The NFPS is designed to develop an ecologically sustainable forestry industry in Australia through:

- removal of unnecessary impediments to market efficiency and access to forests
- development of flexible timber allocation systems through competitive bidding arrangements
- security of supply through clearly defined and tradeable timber harvest rights.

Implementation of the NFPS is being achieved through the development of Regional Forest Agreements (RFAs) between the Commonwealth, State and Territory Governments, and export of hardwood woodchips beyond the year 2000 is conditional on having RFAs in place. The RFAs are negotiated through an open process involving a range of stakeholders, including scientists, economists, conservationists, industry and community groups and

Table 30. Production of various forest products in Australia (adapted from ABARE, 1997).

Timbers	1995/96 ('000 m^3)	1996/97 ('000 m^3)
Sawnwood (coniferous)	2053	2062
Sawnwood (broadleaf)	1391	1321
Railway sleepers	86	72
Plywood	131	151
Particleboard	826	790
Medium density fibreboard	377	434
Total	*4865*	*4830*
Papers & Paperboard	1995/96 (kt)	1996/97 (kt)
Newsprint	445	421
Printing & writing	351	364
Household & sanitary	180	181
Packaging & industrial	1344	1452
Total	*2320*	*2418*

political groups (Department of Primary Industry, Forestry, 1998). They are intended to deliver certainty of conservation outcomes, balanced by security of access to resources for industry. A major summary of the current state of Australia's forests is expected to be released in late 1998 (Commonwealth of Australia, 1998).

The Australian Bureau of Agricultural & Resource Economics produces a quarterly report, *Australian Forest Products Statistics*, giving details of various categories of forest production. According to a recent issue (ABARE, 1997), Australia in 1996/97 exported 57 200 cubic metres of sawn wood, and consumed 4 082 100 cubic metres, about one third coniferous and two thirds broadleaf. Production of sawn timber amounted to 1 954 600 cubic metres of exotic conifers, 101 300 cubic metres of Cypress Pine, 5900 cubic metres of Hoop Pine, 400 cubic metres of Tasmanian conifers, 1 314 300 cubic metres of *Eucalyptus* and 10 200 cubic metres of other broadleaf species. Imports of all types of sawn timber in 1996/97 was 756 300 cubic metres (ABARE, 1997). Production of various forest products in Australia for 1995/96 and 1996/97 is given in Table 30.

Eucalyptus

Eucalyptus species form the basis of the Australian hardwood timber industry. Various species are used for building and construction, furniture manufacture, railway sleepers and craft work, as well as in processed products ranging from plywood and particle board to paper.

Eucalyptus is extensively planted abroad as a timber crop. Eldridge *et al.* (1994) point out that at the beginning of the 1990s the largest *Eucalyptus* plantations in the world (3 million hectares) were in Brazil, with further large areas in India, Spain, Portugal, South Africa, Angola and China. Poynton (1979) provided details of the c. 200 species of *Eucalyptus* planted in southern Africa for timber, oil and pulp, and statistics on their performance in trials in different countries. In Australia the area of *Eucalyptus* plantations to 1989 was 55 000 hectares with another 30 000 hectares of reseeded harvested native forests (ABARE, 1990).

Recently, selected *Eucalyptus* clones have been re-imported to Australia to improve plantation timber yields. For example, Lake (1998a) described *Eucalyptus grandis*/*E.camaldulensis* hybrid clones imported from Brazil.

Paper

The earliest paper mills in Australia were based on locally grown *Pinus radiata* pulp, and imported pine pulp (Grant, 1989). Since the 1960s, with the development of methods to produce chemical Kraft pulp from the wood of *Eucalyptus* species, an increasing quantity of chipped timber from eucalypt forest has being going to paper production, both within Australia and overseas. The processes used are described by Higgins (1978). ABARE (1997) reported exports of 3 323 200 tonnes of woodchips in 1996/97, worth $543.5 million. Abroad, in addition to *Eucalyptus*, Australian *Acacia* species, particularly *A. mearnsii*, *A. saligna* and *A. mangium*, have been planted in over 70 countries, mainly as a quick source of pulp for paper making. J.Turnbull *et al.* (1997) reported that these plantations covered about 2 million hectares.

Hardboard

Eucalyptus spp. are also used in the manufacture of hardboard, usually referred to by its trade name of Masonite. The process, invented by W.H.Mason in Mississippi in 1926 to process pine waste into a composite board, has been used in Australia since 1939 to convert sawmill waste to board (Grant, 1989). Both wood and bark can be incorporated into the product. A different process, using an Asplund Defibrator, is used in some factories (Macmillan, 1978; Grant, 1989).

Timber

Eucalyptus is the basis of the Australian hardwood timber industry. The yield of sawn hardwood in Australia in 1996/97 was 1.3 million cubic metres, most of it *Eucalyptus*. Hillis & Brown (1978) provided an overview of the *Eucalyptus* timber industry. The total annual harvest of *Eucalyptus* wood in Australia in 1994 was 13 million green tonnes, of which only about 1% came from plantations (Eldridge *et al.*, 1994).

As well as *Eucalyptus*, other genera are or have been utilised for a range of purposes, and some of the most important are discussed briefly in the following paragraphs. A large number of Australian forest trees are used in small quantities in the craft industry and specialist furniture industry (e.g. *Allocasuarina fraseriana*, Jones, 1998). Many of these are discussed by Cribb & Cribb (1982) and Doran & Turnbull (1997). Bootle (1983) provided detailed data on the properties of Australian timbers.

Huon Pine

Huon Pine (*Dacrydium franklinii*) was the basis for a major timber industry in Tasmania from about 1816. It was recognised as an excellent construction timber, particularly for specialised uses such as boat and ship building. The timber is very fine-grained and is impregnated with an oil that makes it very resistant to rotting. The oil (methyl eugenol) was extracted from sawdust and scrap timber, and used as a disinfectant, insecticide, analgesic and skin treatment. Huon Pine is noted for being one of the most long-lived of plants. Individual trunks more than 2200 years old are known (Burrows, *et al.*, 1977), and individual clones are suspected of being very much older. However, it takes about 500 years for a tree to mature, making plantation growth impractical. Harvesting of the natural resource was intensive from 1816 until about 1880, and revived in 1890–1900. The last major harvest was in the 1970s when timber to be submerged by hydroelectricity dams on the Gordon River was salvaged and stockpiled. Small quantities of sub-fossil logs are still collected under licence from rivers and beaches. The species is well reserved in western Tasmania (Pedley *et al.*, 1980), but is unlikely ever again to be a major timber resource, other than in the craft industry.

Hoop Pine

Plywood production in Australia was originally based on *Araucaria cunninghamii* (Hoop Pine) but as supplies of this timber from native forests became scarce other rain forest timbers and imported species were substituted (Grant, 1989). More recently *Pinus radiata* from plantations has been used, and about 10% of plywood production now uses *Eucalyptus* spp. (Wade & Ksiazek, 1990).

Hoop Pine was recognised very early as a valuable timber, being used for joinery and shelving, and because of its odourless timber, for butter boxes. Plantations were established in New South Wales from the 1920s, with limited production from plantations being harvested from 1961. Extensive plantations of Hoop Pine were also established in Queensland, although exotic pines are now favoured for their quicker growth and ability to grow on poorer soils (Cribb & Cribb, 1982).

Cypress Pine

Callitris glaucophylla (syn. *C. glauca*, White Cypress Pine) was formerly widespread throughout western New South Wales and south-western Queensland, where it was prized for its high durability and resistance to termite attack. Minor stands occur in Victoria, South Australia, the Northern Territory and Western Australia. In New South Wales *C. glaucophylla* forests are primarily managed for timber production (Lacey, 1973), mainly for building construction, and some plantations have been established (Grant, 1989). About 102 000 cubic metres of *C. glaucophylla* timber was produced in New South Wales in 1987/88, about 5.5% of total sawlogs for that State (Grant, 1989). In Queensland, the harvest has remained steady at about 180 000 cubic metres per annum since 1970 (Department of Primary Industry, Forestry, 1998).

Blackwood

Acacia melanoxylon (Blackwood) extends from Queensland through New South Wales, Victoria and Tasmania to South Australia. In Tasmania and Victoria it reaches 30 m tall, and is a prized cabinet making and craft timber, resembling teak (Cribb & Cribb, 1982; New, 1984). It is easy to work, although some people develop allergies to the dust. Production in Tasmania in 1990 was 16 000 cubic metres per annum, mainly from old growth forests (Allen, 1992). Blackwood has been grown as a plantation timber for some years in New Zealand (Nicholas, 1981, 1988; Gleason, 1986) and South Africa (De Zwaan & van der Sijde, 1990), and matures in 40 to 70 years. It is also grown in a number of other countries (Hawai'i, Sri Lanka, Pakistan, India, Kenya, Malawi, Zimbabwe, Uganda, Tanzania, Congo, Ethiopia, Spain, Portugal, Cyprus, Chile, Argentina and Uruguay) either for timber or pulpwood (Allen, 1992; Doran & Turnbull, 1997). In the late 1980s trials on plantation growth of Blackwood in Tasmania were conducted, with a view to making the entire industry plantation based within 35 years (Allen, 1992).

Other *Acacia* spp.

Acacia aulacocarpa is distributed from northern and eastern Australia to Papua New Guinea. Along with some closely related species it is being evaluated as a source of quality timber, pulpwood and fuelwood in subtropical and tropical regions. Plantations have been established in Australia, China, Fiji, Indonesia, Kenya, Laos, Malaysia, Philippines, Thailand, Vietnam and Zimbabwe (Gunn *et al.*, n.d.; Turnbull, 1987; Thomson, 1994; Maslin & McDonald, 1996; Doran & Turnbull, 1997).

Acacia mangium, another species of northern Australia and Papua New Guinea, is also showing promise as a reafforestation species for timber and pulpwood in subtropical and tropical regions (Turnbull, 1987; Maslin & McDonald, 1996; Doran & Turnbull, 1997).

Sandalwood

Two species of *Santalum* provide the basis of the Australian sandalwood industry. The major source is *Santalum spicatum*, found in Western Australia and western South Australia; smaller quantities of *S. lanceolatum* from northern and western Western Australia and northern Queensland are also exported. The wood is used for joss-stick manufacture, and Australia supplies most of the world market.

Western Australia is the major exporter, through a single company, the Australian Sandalwood Company. Exports in 1989 were 1960 tons, worth $11 480 875 (Statham, 1990). For a short overview of the international trade, see Coppen (1995).

Collection is by pulling out the whole tree, including the stump and larger roots. Roots and butts are the most valuable portion, with the greatest concentration of oils, but the upper trunk and branches are also processed. All supply comes from wild harvesting, on crown land and pastoral leases. Regulations control the size of trees to be harvested. *S. spicatum* takes up to 80 year to mature in the wild and 1985 estimates put the life of the industry at c. 25 years at the then current rate of harvesting.

Studies of sandalwood regeneration in the wild show that there is potential for reseeding to re-establish the species for harvesting in areas where it has been taken formerly (Loneragan, 1990). Limitations on re-establishment include the necessity for several years of good seasonal rains, and the availability of suitable host plants (*Santalum* is a root hemiparasite). Barrett & Fox (1996) suggested establishment of sandalwood as part of salinisation-reduction tree planting programs. Experimental plantations of both *S. spicatum* and *S. album* (high quality oil production) have been established (Statham, 1990).

Charcoal

Charcoal production is one of the more exotic industries based on forest products. Charcoal production from a range of genera (mainly *Acacia* and *Eucalyptus*) in New South Wales was described by Humphreys & Ironside (1980). The charcoal is used to make carbon bisulphide (viscose rayon industry), for case-hardening steel, metallurgy, as fuel for foundries and barbeques, and for the manufacture of briquettes and activated carbon for filters. Charcoal from *Eucalyptus* is used to a large extent in the Brazilian iron and steel industry (Humphreys & Ironside, 1980; Eldridge *et al.*, 1994).

Firewood

Wood for cooking and heating has been a traditional use for native timber for thousands of years. Indigenous peoples used relatively small quantities, but with European settlement usage increased rapidly. Grant (1989) reported that in New South Wales alone, firewood use peaked in the years 1924 to 1940, when up to 600 000 cubic metres of timber was used annually for firewood. Since 1968/69 usage dropped to below 50 000 cubic metres per annum (Grant, 1989). FORTECH (1989) estimated Australia's annual fuelwood collection (mainly *Eucalyptus*) at more than 4 million tonnes, air dried. The Resource Assessment Commission (1992) estimated that firewood collection in Australia had risen to 6.1 million tonnes per annum, and Low (1995) considered that this level of consumption of firewood exceeded ecologically sustainable levels. Neagle (1994a) suggested that 60 000 to 70 000 wood heaters were sold each year in Australia.

In South Australia, New South Wales and Victoria the use of the lignotubers of mallee *Eucalyptus* species as domestic fuel wood was a major industry in the late 19th and first half of the 20th century. These 'mallee roots' were ploughed up for many years after clearance of mallee woodland for agriculture, particularly in the Murray Mallee, Yorke and Eyre Peninsula areas of South Australia. While still used for this purpose, the supply is now dwindling.

Eucalyptus is frequently grown overseas as a source of firewood. *E. globulus* is one of the most usual fuelwood species, being quick growing and providing a good fuel. It is grown for this purpose in Portugal and the Nilgiri Hills of India (Cribb & Cribb, 1982). *Acacia* plantations have been established in many countries, including Kenya, Tanzania, Zimbabwe, People's Republic of China, Thailand, Malaysia and Sabah, principally as firewood sources, but also as food crops, for timber, and to enhance nitrogen fixation in soils (Turnbull, 1987). Midgley *et al.* (1986) provided information on fuelwood species for salt-affected areas.

Native pasture and fodder

A very large part of the Australian pastoral industry is based on native plants. The main taxa involved are Mitchell Grass (*Astrebla* spp.), Saltbush (*Atriplex* spp.), Bluebush (*Maireana sedifolia*), Wallaby Grass (*Austrodanthonia* spp.), Spear Grass (*Stipa* spp.), Tussock grasses (*Poa* spp.) and Kangaroo Grass (*Themeda triandra*).

Four species of *Astrebla* provide the main grazing resource for the summer rainfall area stretching from the black soil plains of western Queensland and north-western New South Wales through the Northern Territory to Western Australia. In the more temperate winter rainfall regions of southern Australia the main native pasture grasses are the danthonioids (particularly *Austrodanthonia*) and *Stipa*. *Themeda triandra* was once widespread throughout Australia, but is very palatable and susceptible to over-grazing and has now all but disappeared from much of its previous range. In subalpine areas of New South Wales, Victoria and Tasmania a substantial summer grazing industry was built on alpine tussock grasses, principally *Poa labillardieri* and *P. sieberiana*, but including many others. With reservation of much of the high country in recent decades, and exclusion of stock from mountain pastures, this part of the industry is now in decline. The contribution of grasses to Australia's economy is discussed in more detail by Lazarides (in press).

In semi-arid Australia, particularly on soils prone to salinisation, extensive shrublands of *Atriplex nummularia* and *Maireana sedifolia* support a major grazing industry. During wetter periods stock preferentially graze on ephemeral herbs and grasses, but in times of drought the chenopod shrubs provide a nutritious and moderately palatable substitute. However, the shrubs are susceptible to over-grazing and trampling, and in the past these shrublands have been degraded. Substantial research has now provided management techniques which can maintain the semi-arid shrublands in good condition. Lambs fed on these shrubs provide meat which is marketed as a specialty product in conjunction with the 'bush food' trade.

Cribb & Cribb (1982) list a number of shrubs and trees which provide a subsidiary resource for stock, either through browsing, or more usually, after lopping or felling to provide fodder during drought. These shrubs and trees include Mulga (*Acacia aneura* and related species), Myall (*Acacia pendula*), Red Ash (*Alphitonia excelsa*), Whitewood (*Atalaya hemiglauca*), Grey Mangrove (*Avicennia marina*), Bauhinia (*Lysiphyllum carronii*), Kurrajong (*Brachychiton populneus*), Bottle Tree (*Brachychiton rupestris*), *Capparis* spp., *Dodonaea* spp., *Ehretia saligna*, *Eremophila* spp., Leopardwood (*Flindersia maculosa*), Wilga (*Geijera parviflora*), Queensland Sandalwood (*Santalum lanceolatum*), Rosewood (*Terminalia volucris*) and Vine Tree (*Ventilago viminalis*). Other accounts of native shrubs and trees used for fodder are those of Wilcox & Morrissey (n.d.), Everist (1969), Askew & Mitchell (1978), Vercoe (1987) and Goodchild & McMeniman (1987).

Essential oils

An overview of aromatic oils extracted from native Australian plants was provided by Cribb & Cribb (1982). They pointed out that one of the first exports from Australia was oil distilled from *Eucalyptus piperita* by John White in 1790.

Currently, major oil production from Australian species is of *Eucalyptus* oil (mostly produced overseas) and Tea-tree oil (of which Australia is the major producer). Minor oil products for perfumes, after-shaves and other cosmetics come from *Backhousia citriodora* (Lemon Myrtle) (Archer, 1997; Costin, 1997; Lake, 1998b), *Boronia megastigma* (Peterson & Evans, 1996) and *Tasmannia lanceolata* (Peterson & Evans, 1996; Peterson, 1998). Sandalwood oil from *Santalum spicatum* was produced in Western Australia until 1971 (Loneragan, 1990). There is potential for this to resume if plantation production of *S. album* is successfully established (Statham, 1990). Other plants with essential oil potential have been tested but are not in commercial production.

One of the problems with production is the different chemotypes within a species, and wild production from plants of unknown chemotypes is a limiting factor. Plantation-grown clones or seedlings from selected seed reduces the variation in chemical composition and oil yields (Boland, 1991; Payne, 1998).

Bulk extraction is usually by steam distillation (*Eucalyptus* and Tea-tree). Solvent extraction is a more expensive method and is used mainly for smaller, high value production, particularly *Boronia* and *Tasmannia* (Peterson & Evans, 1996)

Eucalyptus Oil

Eucalyptus oils are obtained by distillation. Their main uses are in pharmaceuticals, confectionary, toiletries, fragrances, insect repellants and industrial solvents. Use as an additive to ethanol/petrol fuels is under investigation. For a history of the *Eucalyptus* oil industry in Australia, see Boland (1991).

World production is about 3000 tonnes per annum (Peterson & Evans, 1996), of which only 5–10% is produced by Australia (Boland, 1991). The major producer and exporter of oils is China (1600 tonnes/annum), mainly from *E. globulus*. Australia produced about 1000 tonnes/annum in 1939/48, but is now only producing about 110 tonnes/annum, mainly from *E. polybractea* plantations in Victoria and New South Wales. Other countries with a eucalypt oil industry are Portugal, Spain, India, Brazil and South Africa, with minor production in Bolivia, Uruguay, Paraguay, Swaziland, Zimbabwe and Nepal (Coppen, 1995).

The main Australian commercial species is *E. polybractea*, followed by *E. dives* and *E. viridis*. Overseas *E. globulus*, *E. smithii* and *E. citriodora*, and lesser quantities of *E. camaldulensis*, *E. cneorifolia*, *E. dumosa*, *E. elata*, *E. exserta*, *E. goniocalyx*, *E. leucoxylon*, *E. macarthurii*, *E. olida*, *E. oleosa*, *E. radiata*, *E. sideroxylon*, *E. staigeriana*, and *E. tereticornis* are the main commercial crops (Boland, 1991; Coppen, 1995; Woodley, 1998). In overseas plantations oil can be a secondary product from trees grown for fuel, pulp or other purposes.

There is a continuing program of research into eucalypt oils, in search of new products and uses and for improved production. Brophy *et al.* (1991) provided a detailed analysis of the essential oil components of 111 northern and eastern Australian species of *Eucalyptus*, and Lassak *et al.* (1991) summarised the oils of most *Eucalyptus* species.

Tea-tree Oil

Tea-tree oil is produced principally from *Melaleuca alternifolia*, although *M. linariifolia* and *M. dissitiflora* are sometimes used (Colton & Murtagh, 1990; Drinnan, 1998; Woodley, 1998). *M. alternifolia* occurs naturally along coastal regions of northern New South Wales and southern Queensland, and was wild-harvested until the 1980s, when plantations began to be established. The oil has anti-bacterial and anti-fungal properties and is used in toiletries and healthcare products, especially in mouthwash, antiseptic creams, shampoos and soap.

Production of oil in 1989 was 55 tonnes, rising to approximately 150 tonnes in 1995 (Peterson & Evans, 1996). Australia consumed about 20 tonnes per annum in 1989–1991. About 80% of the crop is exported, mainly to the USA (Downing, 1994). The main plantations are in northern New South Wales where projected production is 500 tonnes by the year 2000. Smaller plantations have been established in Queensland, particularly in the Atherton Tablelands where the crop is seen as an alternative to tobacco (Kernot, 1994). See Stubbs & Davis (1992) and Drinnan (1998) for overviews of the industry in New South Wales and Queensland respectively. For industry overviews, planning and marketing strategies see Dean (1988), Murtagh & Southwell (1989) and Murtagh (1991).

Trial plantings of *M. alternifolia* for oil extraction have been established in China, Fiji, India, Indonesia, New Zealand, Thailand and the USA (Peterson & Evans, 1996).

Tropical Myrtaceae - *Asteromyrtus, Callistemon, Melaleuca*

Thirty six tropical Australian species from these three genera were surveyed for potentially valuable commercial essential oils by Brophy & Doran (1996). Among the species included in the survey were *Melaleuca leucadendra* (as *M. cajuputi*) used as the source species for the cajuput oil industry in Indonesia, and *M. quinquenervia*, the basis for the niaouli oil industry in New Caledonia.

Boronia

The oil of Brown Boronia, *Boronia megastigma*, is obtained from the flowers, mainly by solvent extraction. It is used mainly in flavouring (and to a lesser extent in perfumery). The industry was originally based on extraction from wild-collected material in Western Australia, but is now mainly centred on plantation-grown clones in Tasmania. Limited production occurs in New Zealand. Production was less than 0.5 tonnes in 1995 (Peterson & Evans, 1996) but the value of the absolute oil is over $10 000 per kg.

Tasmannia

Tasmannia lanceolata (Native (Mountain) Pepper) is primarily utilised as a bush food, but an oil extract has been produced and is being marketed as a flavouring in chewing gum and toothpaste in Japan. Marketing research into other applications in the food industry is continuing (Peterson & Evans, 1996; Padbury, 1998).

Olearia

Olearia phlogopappa (Dusty Daisy Bush) is a variable, aromatic plant, grown mainly for its colourful flowers. Trial extractions of oil from this plant are currently being evaluated (Peterson, 1998).

Sandalwood

A small Sandalwood oil industry existed in Western Australia until 1971, based on *Santalum spicatum*. The oil of this species is inferior to that of *S. album* from east India, although *S. album* oil can be approximated by blending oil from *S. spicatum* and *S. lanceolatum* (Loneragan, 1990). *Santalum album* is native from India to Hawai'i and extends to coastal Northern Territory (George, 1984c). Investigations of the possibility of establishing plantations of *S. album* are underway (Statham, 1990)

Native plants for revegetation

Since European settlement of Australia, large areas of the natural vegetation have been cleared for agriculture, forestry, mining and urban development (see Cresswell, this volume; Fox, this volume; Glanznig, 1995). Increasing environmental concern has led to the expectation that mining areas (especially open-cut mines) will be returned to something approaching their natural state after the minerals have been extracted. In the case of degraded agricultural land, the emphasis is usually on returning the land to productivity, through agroforestry or pasture establishment.

In the case of mine-site rehabilitation there is often a requirement for selection of plants with high tolerance of heavy metals, extreme pH tolerance or other extreme ecological conditions. A new journal of the Australian Minerals and Energy Environment Foundation (AMEEF), *Groundwork*, was established in 1997 to disseminate information in this field.

It is estimated that there are c. 32.4 million hectares of saline land in Australia, 28.2 million hectares of which is natural (salt lakes, coastal marshes etc), with the remaining 4.2 million hectares being created by agricultural practices since European settlement. About 3.8 million hectares is referred to as 'scalded', where the loss of topsoil has exposed the saline subsoil; the rest is affected by seepage salinity, where the watertable has risen after clearing of vegetation, particularly trees (Robertson, 1996). An additional 250 000 hectares of land is salt-affected in irrigation areas of New South Wales. To repair areas subject to salinisation requires selection of strains and species that are salt tolerant (Fraser *et al.*, 1996; Barrett & Fox, 1996), and adoption of new methods of land management (Beal, 1993; Gomboso *et al.*, 1996; Hamilton & Bathgate, 1996). Replanting of trees (preferably of local provenance) will reduce recharge of watertables and related salinisation (Hamilton & Bathgate, 1996).

Doran & Turnbull (1997) provided descriptions and horticultural details for a wide range of native trees and shrubs suitable for land rehabilitation in the Australian tropics. Marcar *et al.* (1995) and Midgley *et al.* (1986) provided additional information for salt-tolerant tree species for tropical and temperate areas. Socioeconomic aspects of maintaining native vegetation on agricultural land were examined by Price (1995).

In the last decade a number of State, Territory and Commonwealth Government programs have been established to rehabilitate and revegetate degraded areas. Most of these programs involve a large community component, and seek to work with landowners for mutual benefit. These programs include national and State Landcare programs, various State Remnant Vegetation Protection and Revegetation schemes, One Billion Trees, Save the Bush, and several programs under the Natural Heritage Trust, including Bushcare.

Miscellaneous uses

Honey

Honey from native bee nests was a sought-after delicacy of the indigenous peoples. The techniques for gathering it are described by Isaacs (1987). Indigenous peoples also extracted nectar directly from a range of flowers, by sucking inflorescences or dipping them in water. *Grevillea*, *Banksia* and *Hakea* were the main sources of nectar (Isaacs, 1987; Latz, 1995).

Use of the native Australian flora as a source of nectar and pollen for honey production by the introduced honey bee, *Apis mellifera*, is 200 years old. From a cottage craft it has expanded into a sizeable industry, supplying both commercial bulk honeys and specialist products based on particular species. Among the latter are Leatherwood honey (derived from Tasmanian *Eucryphia* spp.), River Red Gum honey (*Eucalyptus camaldulensis*) and Yellow Box honey (*Eucalyptus melliodora*). Both native and introduced plants contribute to the honey industry, although the native species predominate. The number of taxa involved is quite high. For New South Wales alone, Clemson (1985) listed over 300 species, about two thirds of which are native. The most important are numerous species of *Eucalyptus*; of somewhat lesser importance are *Angophora*, *Lophostemon*, *Melaleuca*, *Callistemon*, *Leptospermum*, *Banksia*, *Acacia* (pollen only), *Casuarina*/*Allocasuarina* (pollen), *Eucryphia* and some mangroves.

In 1994/95 honey production in Australia was 19 000 tons, worth $24 621 000 (McLennan, 1997).

There is a very large literature on the honey flora. The following are just a sample of recent and older works: Australia: Rayment (c. 1917), Cribb & Cribb (1982); New South Wales: Goodacre (1958), Clemson (1985); Queensland: Blake & Roff (1988); Victoria: Department of Agriculture (n.d.); South Australia: Purdie (1968).

Wattle Bark

One of the first industries established in Australia after European settlement was a tanning industry to produce leather. The industry was built on tannins extracted from the bark of a number of native taxa, principally *Eucalyptus* spp. A Government tan yard was established in Parramatta in 1801, and by the following year sample shipments of tan bark were being sent to England for evaluation. By 1814 *Acacia* spp. had been identified as an excellent source of tan bark, and by 1828 *Acacia mearnsii* or Black Wattle (then known as *A. decurrens* or Green Wattle) was established as a high quality and abundant source.

In the period 1840 to 1905 large bark stripping and processing industries were established in southern New South Wales, in south-western and north-eastern Victoria and in eastern Tasmania. At the peak of this industry, up to 20 000 tonnes of wattle bark per annum were exported. A Board of Inquiry into the industry in Victoria in 1878 found that at that time about 12 000–15 000 tonnes of wattle bark was harvested annually to support the Victorian tanning industry. As all of this had come from wild-harvesting, and killed the trees involved, widescale destruction of the resource had occurred. From 1883 a number of Government-sponsored plantations were established in Victoria, South Australia and New South Wales and these continued to be established until about 1920. Private plantations continued to be established until about 1943. However, fires, a declining market, competing land uses, high stripping and transport costs, and a lack of a market for the wood, all contributed to their eventual failure.

South Africa established more successful plantations of *Acacia mearnsii* from the 1880s, and by the 1940s was a major exporter. Plantations totalled about 400 000 hectares (Cribb & Cribb, 1982). Even Australia imported tannin extracts from *A. mearnsii* from South Africa, with a peak of 16 887 tonnes of bark and extract in 1944. Brazil also became a major exporter from *A. mearnsii* plantations in the 1980s. Since 1984 China (in collaboration with Australia's CSIRO) has also established plantations of this species, to service its domestic tanning industry. Other countries growing *A. mearnsii* for tan bark are Kenya, Tanzania, Zimbabwe, Indonesia, the Philippines and Sri Lanka (Cribb & Cribb, 1982).

Chromium salts, either alone or in combination with tannin, were increasingly used as a faster and cheaper tanning method during much of the 20th century. This contributed to the decline of the tan bark industry. From the 1950s, leather production declined sharply, as synthetics were increasingly used for furniture and shoes, and demand for other leather products, such as harnesses, declined.

From the 1960s, however, there has been something of a resurgence in the tan bark industry. Concerns about heavy metal contamination have reduced the popularity of chromium-based tanning processes, and a new industry has developed: the production of waterproof glues based on phenol-formaldehyde fortified *A. mearnsii* tannins. These are used increasingly in the production of water resistant plywoods and particle boards.

In 1984 a major research project on *A. mearnsii* biology, silviculture, properties, chemistry, production and use of tannin extract and prospects for its development as an industry in China, was established between the Chinese Academy of Forestry and the Australian Centre for International Agricultural Research. The major outcomes of this research were described in a Chinese-language publication in 1991. This was reissued in abridged form, in English, in 1997 (Brown & Ho, 1997). New (1984) provided a history of the industry in Australia and abroad, and information on chemistry, plantation sizes, and yields. Grant (1989) traced the history of the wattle bark industry of New South Wales, and Luyt *et al.* (1987) described the production of wattle bark from *A. mearnsii* in Zimbabwe. A comprehensive history of the Australian *A. mearnsii* wattle bark industry was written by Searle (1991). Doran & Turnbull (1997) provided detailed silvicultural information for the species, both within Australia and abroad.

Cribb & Cribb (1982) listed other taxa used as a source of tan bark as *Acacia pycnantha*, *Bruguiera spp.*, *Callitris* spp., *Casuarina* spp., *Eremophila longifolia*, *Eremophila oppositifolia*, *Eucalyptus alba*, *Eucalyptus astringens*, *Eucalyptus calophylla*, *Eucalyptus diversicolor*, *Eucalyptus gomphocephala*, *Eucalyptus wandoo* and *Rhizophora stylosa*.

Brush Fencing

The construction of domestic fencing from bundles of 'brush' has been popular in South Australia (particularly Adelaide) since at least the 1940s. From about the mid-1970s, the practice spread to the eastern States. Brush fencing is a prestige product, costing at least 30% more than the most expensive sheet metal product, but about half the price of a reinforced brick fence of comparable height.

Brush fencing is made from the thin flexible stems of *Melaleuca uncinata*, sometimes with the addition of *Baeckea behrii*. Fences are typically 1.5 to 2 m tall, and weather to an attractive dark grey. If well constructed they have a life of 20 years or more, and because of their high oil content, are resistant to rot and termites. On the other hand, they are very flammable, and can harbour insect pests.

Supplies of brush for Adelaide come from wild harvesting, principally in the Murray Mallee and South East of South Australia (mainly the Pinnaroo–Lameroo area) and from western Victoria. Supplies for the Sydney market are cut near West Wyalong in New South Wales. Lewis (1979) estimated that at that time about 1800 tonnes of brush were used in Adelaide per annum, and this figure was supported by another study by Bastin *et al.* (1982). These figures translate to the harvest of about 6000–9000 plants per week, or 100 to 300 hectares per annum. Woodley (1998) set usage at the equivalent of 30–50 km of fencing per annum. More than 70% of plants regenerate after harvesting, mimicking their behaviour after fire. Regeneration periods of 10 years after fire or harvesting are required to produce commercial-sized stems, and individual plants may therefore be capable of providing 3 or 4 crops in an estimated lifespan of 50 years. The continuing supply of material is largely dependent on natural regeneration. Very small trial plantation plantings near Monarto by the South Australian Woods & Forests Department were reported by Bastin *et al.* (1982), and others at Dimboola, Lameroo and other sites in south-eastern South Australia were reported by

Bulman *et al.* (1998), but no commercial plantations appear to have been established. Bulman *et al.* (1998) examined the economics of plantation farming of *M. uncinata,* and reported a usage rate of about 100 000 bundles (each of 23 kg) per annum for Adelaide alone.

The economic value of the industry has not been estimated, although Bastin *et al.* (1982) reported 24 brush fence companies operating in Adelaide in 1982, mostly family businesses. The value of the brush used was $156 000 to $468 000 per annum to the cutters. Construction costs were 2–3 times this amount, making the industry worth perhaps $2 million per annum in South Australia alone in 1982. Woodley (1998) cited concerns that the industry was not sustainable, although the South Australian Government disagreed.

Dye Plants

In the early years of European settlement many plants were investigated as sources of dyes for cloth, but following the development of aniline dyes in the 1860s, and the subsequent replacement in industrial use of most natural dyes by synthetic ones, the search was largely abandoned (Cribb & Cribb, 1982). Some plants of historical interest, including some traditional Asian dye plants, are discussed by Cribb and Cribb (1982).

Since the 1960s an increased interest in fibre crafts, especially spinning and weaving, has revived the interest in native plants as dye sources. In addition to the information collected in the nineteenth century, Spinners and Weavers Guilds in several States have coordinated tests of local plants and several books are available, e.g. Lloyd, 1971; Handspinners & Weavers Guild of Victoria, 1974; Carman, 1978; Trendall, 1981. Hundreds of native plants produce useful dyes, in particular species of *Eucalyptus* and *Acacia*.

Gums, Resins and Kinos

A number of native plants produce exudates, and many of these were used by indigenous peoples as foods, cements and gums. Relatively few have been exploited commercially, the one exception being the resin from *Xanthorrhoea* spp. This resin is produced copiously at the base of the leaves, and has been used in the manufacture of picric acid (for explosives), as an (inferior) substitute for shellac, as a varnish for metal instruments, and in stove polish, incense, perfumery, soap, sealing wax, paper sizing and in gramophone record and linoleum manufacture. An industry to collect this resin, based on *X. resinosa* (New South Wales and Victoria), *X. preissii* (Western Australia and *X. tateana* (Kangaroo Island, South Australia), previously existed, and at its peak in about 1940 over 2500 tonnes of resin per annum was being exported (Neagle, 1994b). The Kangaroo Island industry still exists, with production also resuming recently on a very small scale in Western Australia (Neagle, 1994b). In 1994 exports of Yacca (*Xanthorrhoea*) resin from South Australia were about 153 tonnes, with a further 30 tonnes being produced in Western Australia. The industry was estimated to have a life of about 20 years (Neagle, 1994b). However, Woodley (1998) reported that the industry on Kangaroo Island had now ceased. Cribb & Cribb (1982) provide descriptions of other species yielding gums, resins and kinos of minor importance. Cribb & Cribb (1975) and Low (1991) describe *Acacia* gums which were and still are used as food or in drinks. Isaacs (1987) and Latz (1995) mentioned that gum from *Casuarina*/*Allocasuarina* is also eaten, and Latz also identified *Crotalaria eremaea* as a source of edible gum. New (1984) provided information on the chemical constituents of *Acacia* gum.

Soap Making

Various species have been burned to produce the alkaline ash or barilla necessary as an ingredient in soap making (the other ingredient is fat or oil). Cribb & Cribb (1982) described the use of *Avicennia marina* and *Casuarina paludosa* for this purpose. Bird (1981) described the Australian barilla industry based on *Avicennia marina* in Victoria, New South Wales and South Australia in the 1840s and 1850s, and a similar industry based on unspecified mangroves in Moreton Bay during the same period.

Whinray (1981) described the barilla industry in Tasmania. This industry existed from at least 1819, and was based at first on barilla produced by burning kelp. Later, about 1822, *Acacia mearnsii*, *Allocasuarina verticillata* (syn. *Casuarina stricta*) and *Eucalyptus* spp. were used. From 1823 to about 1830 a barilla industry based on chenopod shrubs (particularly *Atriplex cinerea*, *Rhagodia baccata* and *Arthrocnemon arbusculum*) from the east coast of Tasmania and islands of Bass Strait serviced a soap manufacturer called Roberts on Bruny Island, and others in Hobart. By the 1850s chemically produced alkali was available in quantities and of a quality that made the barilla industry uneconomic.

Sphagnum Moss

Woodley (1998) reported on a tiny sphagnum moss harvesting industry that operates in Tasmania, yielding about 125 cubic metres per annum.

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IMAGES OF AUSTRALIAN PLANTS

Helen J. Hewson[1]

People have used plants in their decorative imaging for longer than man's recorded history demonstrates. The flower, in particular, has captured our imagination and provided an escape into a world of beauty, symmetry, and colour far beyond that provided by everyday drudgery. There was nothing new in depicting Australian plants, except the plants themselves.

The first European images of Australian plants were published in 1703 in the context of exploration of the world. Europeans were searching for new lands with new plants for trade and utilisation, and to satisfy curiosity and other scientific endeavour. William Dampier (1652–1715), on the first officially sanctioned English voyage, of the *Roebuck* in 1699, collected some plants in the vicinity of Shark Bay and the Dampier Archipelago, Western Australia, and had drawings of some of these made for his book, *A Voyage to New Holland, &c In the Year 1699* (Dampier, 1703). The artist is anonymous. These drawings were aimed at informing the British government and future mariners of what they might expect to find in New Holland (Australia).

It was not until 1772, when James Cook (1728–1779) returned from his exploration of the Pacific Ocean, including the landings on Australia's eastern shores, that Australian plants began to be known and grown in Europe. The naturalists on the voyage, Joseph Banks (1743–1820) and Daniel Solander (1733–1782), collected plants and their seeds, while Sydney Parkinson (1745–1771) busily sketched them. Unfortunately, although Parkinson's work was prepared for printing (a large number of plates being painted and engraved by Frederick Polydore Nodder (fl. 1770–c. 1800)), it remained unpublished for over a hundred years, until James Britten printed a selection in *Illustrations of Australian Plants Collected in 1770 during Captain Cook's Voyage* (Britten, 1900–1905).

Meanwhile, the British government decided, largely on the advice of Banks, to establish a penal colony at Botany Bay in New South Wales. This was effected in 1788, though the settlement was actually established at Port Jackson. From that time on, Australian plants entered the world of European utilisation, both in Australia and in Europe. At Port Jackson the settlers had to make do with what was available; in England the gardeners, scientists and artists were busy with a new wealth of the exotic. The French, too, were stepping up their interest in the Southern Hemisphere and their voyages stocked French gardens and halls of science.

For the early colonists the only means of communication were words and images. While the scientists struggled with the former, ordinary people, even the convicts, made best use of the latter. John Calaby (1988) has documented the early natural history art of the Colony. Significant collections of the surviving early works are in the Natural History Museum, London, the Mitchell Library, Sydney, and the National Library of Australia, Canberra. In 1989, the National Library of Australia published a bound collection called the *Hunter Sketchbook* (Calaby, 1989). John Hunter (1737–1821), a member of the First Fleet, who became the second Governor of the colony, maintained a sketchbook. Most of the paintings in this are reputed to have been executed by Hunter himself, although other, more competent, artists also made contributions.

Thomas Watling (1762–?1814), transported to Australia in 1793 for forgery, was assigned to the Colony’s Surgeon-General, John White (d. 1832), to make drawings of the local plants, animals and birds. White supplied these drawing to James Edward Smith, who used them to produce the first “Flora” documenting Australia’s plants: *A Specimen of the Botany of New Holland* (Smith, 1793). The engraver of the plates was James Sowerby (1757–1822), who went on to be one of the more prolific illustrators of Australian plants in the early nineteenth century.

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The famous French botanical artist Pierre-Joseph Redouté (1759–1840) also illustrated Australian plants. The first published was *Eucalyptus obliqua*, in L'Héritier's *Sertum Anglicum* (L'Héritier, 1779–1792). More dramatic are Redouté's colour printed stipple engravings in Étienne Ventenat's, *Jardin de la Malmaison* (Ventenat, 1803–04). The latter engravings were based on Australian plants growing in Empress Josephine's garden, her garden being stocked from English gardens and from collections made by Jacques Julien Houtou de Labillardière (1755–1834).

Labillardière was the botanist on the expedition lead by Bruny d'Entrecasteaux (1740–1793) to Australia and the Pacific, in search of La Pérouse, an explorer lost in the western Pacific not long after the arrival of the British First Fleet in Port Jackson. Nicolas Piron (fl. 1791–1797), botanical artist, also accompanied the expedition.

Based on his own collections, and on the drawings made by Piron, Labillardière published the second Australian 'Flora', *Novae Hollandiae Plantarum Specimen* (Labillardière, 1804–1806).

The activities of the French forced the British Government to have the whole Australian coastline surveyed. Matthew Flinders (1774–1814) was appointed for the task, in command of the *Investigator*, and the expedition left England in July 1801. On board were Robert Brown (1773–1858), botanist, Peter Good (fl. 1801–1803), gardener, and Ferdinand Bauer (1760–1826), botanical artist. Bauer made over 1500 drawings of Australian plants, the majority of which have not been published.

Following the publication of Labillardiere's book, Jonas Dryander (1748–1810), Joseph Banks' librarian, published a paper documenting the number of species of Australian plants published to that time (Dryander, 1806). There were 370 and approximately 275 of them had been illustrated at least once. This did not approach the 362 original sketches of Sydney Parkinson, let alone the 1542 drawn by Ferdinand Bauer while on the protracted Flinders' survey. So while the number of published illustrations was apparently large, it was far behind the potential. Bauer aimed to prepare a parallel work to illustrate Robert Brown's *Prodromus Florae Novae Hollandiae et Insulae Van-Diemen* (Brown, 1810), which was the third and by far the most comprehensive Australian 'Flora'. But his *Illustrationes Florae Novae Hollandiae* (Bauer, 1813), publishing 15 plates, was a financial failure, as was Brown's *Prodromus*. Neither of the men went on to complete the documentation of their labours.

A veritable army of English and European artists, engravers and colourists continued illustrating plants from around the world, including from Australia. When Joseph Banks died in 1820, William Jackson Hooker (1785–1865) took a leading role in English botany, together with John Lindley (1799–1865). Both men were artists in their own right and both were associated with the grandly illustrated periodicals of the time, continuing a tradition established by William Curtis (1746–1799). Curtis founded the *Botanical Magazine* in 1787 and it has appeared regularly ever since, becoming *Curtis's Botanical Magazine* upon his death. Hooker was its editor from 1827 till his death. He also produced most of the drawings between 1826 and 1834; the engraver was Joseph Swan (fl. 1821–1872). From 1834, Hooker employed Walter Hood Fitch (1817–1892) as artist and engraver. Fitch went on to become one of the most prolific artists of all time and certainly of Australian plants. He achieved this through his own particular ability to 'reconstruct' the plant from a flattened herbarium specimen where necessary, through his speed and efficiency as a draftsman, and through adopting lithography as his method of plate preparation. Hooker also initiated a number of his own 'periodicals', of which *Hooker's Icones Plantarum* has endured.

Sydenham Teast Edwards (1769–1819), originally an artist for Curtis, began his own periodical, *The Botanical Register*, in 1815. This became *Edwards's Botanical Register* following his death. By 1830 John Lindley became the editor of the *Register* till it ceased publication in 1847. An Appendix to Volume 23, *A Sketch of the Vegetation of the Swan River Colony*, by John Lindley (Lindley, 1839) is of particular significance to Australian botany. Lindley also produced a number of important illustrated works, many of educational significance, others monographic in genre. He employed a number of artists, of whom Sarah Ann Drake (1803–1857) is particularly noteworthy.

By the time Ferdinand Mueller (1825–1896) became established as Government Botanist in Victoria, the impetus and quality of illustration of the eighteenth and first half of the nineteenth century had waned. While Mueller published world-wide, he was also determined to promote scientific publication in Australia. He therefore organised the first plates of botanical illustration of Australian plants to be drawn and published in Australia. The honour fell to Ludwig Becker (1808–1861): an example of his work is the plate of *Rhus rhodanthemum* in *Transactions of the Pharmaceutical Society of Victoria* (Mueller, 1858). Becker and his contemporary, Frederick Schoenfeld (?1810–1868), were artists and lithographers. Mueller's *Plants Indigenous to the Colony of Victoria* (Mueller, 1860–65), contains a fine collection of Schoenfeld's work, as does *Analytical Drawings of Australian Mosses* (Mueller, 1864). In later Mueller monographic works such as *Iconography of Australian Species of Acacia* (Mueller, 1887–1888), *Iconography of Australian Salsolaceous Plants* (Mueller, 1889-91) and *Iconography of Candolleaceous Plants* (Mueller, 1892) Robert Graff (fl. 1886–1894) was Mueller's artist and lithographer. Graff did more work than Becker and Schoenfeld but his standard was not as high.

Mueller established a network of collectors and artists to assist him with the massive job of collecting and documenting Australia's flora. Among the artists who cooperated with Mueller in this way were Louisa Ann Meredith (1812–1895) who published *Some of my Bush Friends in Tasmania* (Meredith, 1860); Fanny Ann Charsley (1828–1915) who published *The Wildflowers around Melbourne* (Charsley,1867); Louisa Atkinson (1834–1872) who worked with William Woolls; and Ellis Rowan (1848–1922), who had work published in F.M.Bailey's *Comprehensive Catalogue of Queensland Plants* (Bailey, 1909). Rosa Fiveash (1854–1938), working in South Australia, illustrated monographs for J.E.Brown and R.S.Rogers.

Margaret Flockton (1861–1953), a prolific artist, illustrated for Joseph Maiden at the Herbarium in the Botanic Gardens, Sydney, notably *The Forest Flora of New South Wales* (Maiden, 1903–1925) and *A Critical Revision of the Genus Eucalyptus* (Maiden, 1909–1933). Flockton worked at a time when the standard of scientific botanical illustration was in a serious decline. This makes her contribution all the more commendable. In art, Flockton was a contemporary of Margaret Preston (1875–1963), who worked in the genre of fine art, frequently using Australian native plants as her subject.

During the early and mid-1900s most States had a Flora documenting their respective plants. These were illustrated with line-drawings, but most of the work is little more than adequate for the purpose. Research papers were either not illustrated, illustrated with poor line drawings, and/or illustrated with photographs.

Popular and semi-popular floras emerged, some to treat a selection of plants, some with a more general coverage. Thistle Harris’s *Wild Flowers of Australia*, published in 1938 and illustrated by Adam Forster (1850–1928), was reprinted eight times over four decades. Rica Erickson (1908–) published and illustrated her own semi-popular treatments of interesting groups of plants in Western Australia: *Orchids of the West* (Erickson, 1951), *Trigger Plants* (Erickson, 1958) and *Plants of Prey in Australia* (Erickson, 1968). Erickson went on to play an important role in stimulating younger artists to become botanical illustrators. Stan Kelly (1911–) painted nearly all the species of *Eucalyptus*, which were published in two volumes (Kelly, 1969, 1978).

Around the 1970s a revival began. Winifred Mary Curtis (1905–), Nancy Tyson Burbidge (1912–1977), and Hansjoerg Eichler (1916–1992) appear to have been particularly instrumental in this revival, though the stimuli were manifold and included the celebration of the bicentennary of the landing of James Cook on our eastern shores in 1770. Outside Australia William Stearn (1911–) provided a challenge through publishing *The Australian Flower Paintings of Ferdinand Bauer* (Stearn, 1976), presenting Australians with a long overlooked standard, to which local artists could aspire. Curtis worked with Margaret Stones (1920–) on an illustrated *Endemic Flora of Tasmania* (Curtis & Stones, 1967–1978). Nancy Burbidge illustrated her own flora, *The Flora of the Australian Capital Territory* (Burbidge & Gray, 1970), and Eichler encouraged taxonomists to have their scientific research illustrated with quality line-drawing executed by trained artists. Ludwik Dutkiewicz (1921–), Terrence Nolan (1934–), Margaret Wilson (formerly Menadue) (1942–), Gillian Rankin (fl. 1980s), Christine Payne (1949–), Anita Barley (nee Podwyzynski) (fl. 1980–), and others, emerged. They set a very high standard, which is being followed with distinction, and is exemplified in the *Flora of Australia* and in revised State Floras published during the 1980s and 1990s.

The *Flora of Australia*, through the initiative of its Editorial Committee and inaugural Editor Alexander George (1939–), has encouraged the use of painting in our science too. Limited though the outlet is, a number of very talented botanical painters are now working in Australia and some have had their work used as the frontispiece for *Flora of Australia* volumes (e.g. Bryony Fremlyn, this volume).

Botanical artists are now employed by herbaria and like institutions, working freelance, or teaching. At present, artists are employed on the staff of several of the State herbaria, mainly in the production of line drawings: Gilbert Dashorst (1956–) in Adelaide, Will Smith (1954–) in Brisbane, and Lesley Elkan (fl. 1990s) and Nicola Oram (fl. 1990s) in Sydney. Other herbaria and botanists employ freelance artists as work is required. Celia Rosser (1930–) is the science faculty artist at Monash University. A major project of Rosser's is providing a complete set of paintings of *Banksia* species for *The Banksias* (Rosser & George, 1981, 1988). William Cooper (1934–), David Mackay (1958–), Katrina Syme (1947–) and many others are working freelance. Margaret Saul (1951–) and Jenny Phillips (1949–) are important teachers of botanical art. Australia currently has artists equal in ability to those working elsewhere in the world and rivalling the great artists of the late 1700s and early 1800s.

While the scientific record was proceeding apace, others were capturing the images in their own way and for a multitude of purposes: fine art, decorative art, literature, trade marks and emblems.

For fine art, the volume is enormous. Jennifer Phipps has attempted an 'anthology' of flowers and gardens in Australian art in her book *Artists' Gardens* (Phipps, n.d. [1986]). The flower subjects are not all Australian, but many are, and Phipps chose a good selection of significant examples. Paul Jones (1921–1996), although known worldwide for his extraordinarily detailed acrylic paintings of cultivated plants, has also painted some of the plants of his native land.

Jennifer Isaacs, in *The Gentle Arts: 200 years of Australian Women's Domestic & Decorative Arts* (Isaacs, 1987) has documented a wide range of arts and crafts, many of which have employed representatives of the Australian flora as motifs. This is not surprising, given our heritage of using flowers in design, especially for decoration of the things around us. The plethora of objects upon which the images appear is as universal as all of our household items and décor; all of our clothing and adornments; many of our public buildings and churches; our stationery; and some literature.

The methods of creation embrace the full range of creative craft available for home-making:– needlework (embroidery, tapestry); crochet; knitting; craft sculpture (silk, felt and paper flowers, leather embossing, copper embossing, bread dough moulding; cake decorating); 'weaving' (lace, woven tapestry, rug making); sewing (patchwork, applique); painting (stencilling, china painting, flower painting); woodwork (marquetry, carving, poker work); and stained glass. Simultaneously, floral arrangement of cut and dried flowers, both by professional florists and by amateurs, utilises Australian flowers. Norman Sparnon in *The Beauty of Australia's Wildflowers* (Sparnon, 1967) demonstrated how ideal Australian flowers are for the Japanese Ikebana flower arrangement method. Our flowers have been slow to enter the traditional European florist trade, but they are becoming increasingly popular (see Orchard & Wilson, this volume).

Commercially, flowers are used in the design of patterns for textiles (clothing and furnishing) and wall papers, and for stationery.

It is rare for plants to be the subject of fiction, but May Gibbs (1877–1969) made unique characters out of the Gum Nut Babies and the Big Bad Banksia Man, in children's literature (e.g. Gibbs, 1917). However, many books are published depicting our flora in a range of genres, from our own *Flora of Australia*, through to items like *Banksia menziesii* (Nikulinsky, 1992), by Philippa Nikulinsky (1942–), *A Year of Orchids* (Pugh, 1983) with paintings by Clifton Pugh (1924–1990), and *William Fletcher* (Anderson, 1983) by Trevor Anderson, featuring the work of William Fletcher (1924–1983). Some beautiful books on botanical art and artists have been produced, some concentrating on Australian work (e.g. Gooding, 1991), some more general (e.g. Blunt & Stearn, 1994; Rix, n.d., 1981; Sherwood, 1996). Poets, too, have employed plants in their imaging and philosophising, Judith Wright (1915–) being one of the masters—*The Cycads*, *Gum Trees Stripping*, and *The Forest* are evocative examples (Kramer, 1985).

Australia and each of its States and Territories has an official floral emblem. They are: *Acacia pycnantha* (Golden Wattle) for Australia; *Anigozanthos manglesii* (Mangles' Kangaroo Paw) for Western Australia; *Gossypium sturtianum* (Sturt's Desert Rose) for the Northern Territory; *Swainsona formosa* (Sturt's Desert Pea) for South Australia; *Dendrobium phalaenopsis* (Cooktown Orchid) for Queensland; *Telopea speciosissima* (Waratah) for New South Wales; *Wahlenbergia gloriosa* (Royal Bluebell) for the Australian Capital Territory; *Epacris impressa* (Common Heath) for Victoria; and *Eucalyptus globulus* (Blue Gum) for Tasmania. The Australian Coat of Arms also features *Acacia pycnantha*.

The new Australian Parliament House in Canberra, opened in 1988, has many images of native plants. In the foyer a series of beautiful marquetry panels around the walls depicts flowers and plants from all parts of the country. The panels were designed by Tony Bishop, sculptor, in association with the architects Mitchell Giurgola and Thorp, and made by Michael Reuter. Australian flora is also prominent in the Great Hall, in the tapestry, designed by Arthur Boyd and manufactured at the Victorian Tapestry Workshop, and in the embroidery, designed and coordinated by Kay Lawrence.

Peter Luck in his book *Australian Icons* (Luck, 1992) explored the 'things that make us what we are'. He used *Banks' Florilegium* (Anonymous, 1981–1988), a second (complete) printing of Parkinson's plates, as the icon representing our flora, an odd choice considering that it is extremely expensive and not easy to access. Mimmo Cozzolina in *Symbols of Australia* (Cozzolina, 1980) took a different approach. He investigated trade-art and its trade marks and symbols. He determined that the 'gumtree' (*Eucalyptus*) has been used most commonly. The Waratah (*Telopea*), Wattle (*Acacia*), and Black Boy (*Xanthorrhoea*) are commonly used. Kurrajong (*Brachychiton*), Treefern (*Dicksonia*), and Ti-tree (*Leptospermum*) were also identified.

Postage stamps have long been seen as an effective means of publicity/propaganda for a country and Australia has effectively used stamps to promote itself. Yet it is noticeable that the unique Australian flora has been under-utilised in this medium. Although some early Commonwealth stamps used flowers as framing elements, it was not until the higher value definitive set of 1959–1964 that the Australian flora was featured in its own right. This monocolour set included Christmas Bells (*Blandfordia*), Flannel Flower (*Actinotus*), Wattle (*Acacia*), *Banksia* and Waratah (*Telopea*). In 1968 another set of 6 stamps featured the State floral emblems, this time in multicolour. Since then the flora has been more commonly depicted: a highlight of flora stamp issues was the 1986 Australian Bicentennial III: New Holland – Cook's Voyage issue, which features Joseph Banks, Sydney Parkinson and Parkinson's paintings of *Banksia serrata, Hibiscus meraukensis*, *Dillenia alata*, and *Correa reflexa*. The Australian National Botanic Gardens maintains on its World Wide Web site an illustrated index to Australian floral designs on stamps.

In paper currency, the five dollar note, released with the advent of decimal currency in 1966, also featured Joseph Banks and an assemblage of Australian flora.

This brief account touches only on some of the highlights of past and present use of Australian plants in arts, crafts, design and literature. However it does demonstrate the importance of the Australian flora as icons of national identity and its important role in the culture of the nation. As demonstrated elsewhere in this volume, Australia is custodian of a unique suite of plants, one of the megadiverse floras in the world. Such an important resource will undoubtedly be used increasingly in trade, commerce and cultural contexts.

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CONSERVING AUSTRALIA'S FLORA

Ian D. Cresswell[1]

Introduction

European settlement has seen a range of changes to the landscape of the Australian continent over the past 200 years, with major reductions in the area of native vegetation types, particularly through clearing in the eastern and southern agricultural areas. The effects of non-Aboriginal settlement on Australia's flora are apparent throughout the continent, but differ markedly regionally, mostly depending on the dominant land uses that settlers have imposed on the landscape. Those changes, and their flow-on effects, are still happening, and the loss of species and decline in habitat diversity have not been halted. While the last twenty years has seen the recognition of this as a major environmental problem, the actual trend in species decline flowing from many decades of poor management will be with us for some time to come.

The history of conservation of Australia's flora (and fauna) is of course linked to the history of each of the major colonies, which are now the States of Australia. While the federation of these colonies into the Commonwealth of Australia has been in effect for nearly 100 years, the major changes to how we viewed, and then conserved, our natural resources, has only happened since the 1970s. The last 25 years have seen the development of truly national efforts for the conservation of biological diversity, and indeed it is only in the last five years that all governments have signed agreements to put into effect real changes in how we protect native species nationally.

The federal system of government places the vast majority of terrestrial land and coastal sea management responsibilities with the six States (New South Wales, Queensland, South Australia, Tasmania, Victoria, and Western Australia), and the two self-governing Territories (Australian Capital Territory and Northern Territory). Land management responsibilities, of course, include the protection of flora and fauna, which has traditionally been seen as the establishment of protected areas, although in recent years off-reserve conservation, such as the halting or slowing of vegetation clearance, has been a very significant mechanism to combat the loss of native species.

The Commonwealth consistent with the Constitution, has responsibility for certain areas of land, including lands in the Northern Territory and the Australian Capital Territory, which were retained by the Commonwealth at the time that those territories attained self-government. In addition, the Commonwealth has jurisdiction over the land and territorial seas of the Territory of Jervis Bay, the Great Barrier Reef Marine Park, the Australian External Territories, and the Australian territorial sea between a distance of three nautical miles and 200 nautical miles from the coasts of the States and the Northern Territory, known as the Economic Exclusion Zone (EEZ).

The proportion of terrestrial mainland Australia that the Commonwealth directly manages is small, about 0.5% of mainland Australia, the States and Territories directly manage 22.5%, and private owners manage 77% of the total area of mainland Australia, including 14% managed by indigenous Australians (AUSLIG 1993 Public Lands dataset). The Commonwealth is responsible for approximately 95% of the marine estate while the States are responsible for approximately 5%. Despite the differing land tenures, governments (especially the States and Territories) still have responsibilities for conservation on land they don't directly 'own', e.g. endangered plants on private land.

The conservation of flora and fauna in Australia is not restricted to protected areas and other public land tenures. Many private landholdings, including Aboriginal lands, are managed in sympathy with their nature conservation values. However, the amount and diversity of land formally dedicated to nature conservation is one important indicator of our success at protecting our natural heritage. Altogether approximately 7.6% of mainland Australia and 3.5% of the Australian marine environment are protected in statutory protected areas (Cresswell & Thomas, 1997). The Commonwealth manages approximately 3.3 million hectares of terrestrial nature conservation reserves and 36.8 million hectares of marine protected areas. The States and Territories manage approximately 56.4 million hectares of terrestrial nature conservation reserves and 2.2 million hectares of marine protected areas.

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[1] National Land and Water Resources Audit, GPO Box 2182, Canberra, Australian Capital Territory 2601.

Another key measure of flora conservation has been the adoption of controls on vegetation clearance. Constitutionally, and customarily, land management is largely a matter for the States and Territories and the land use controls associated with each tenure type are set by their legislatures. Consequently there is marked variation in land use controls between the States and Territories.

Controls on vegetation clearance in the States and Territories have been introduced for a range of reasons, including the protection of soil and water resources, biodiversity conservation, Aboriginal heritage and aesthetics. The controls that have been introduced in different areas over the past 50 years have had markedly different results in slowing down the rate of biodiversity loss.

The Commonwealth Government also has an important role in the sustainable use and management of land resources. *The National Strategy for the Conservation of Australia's Biological Diversity* (Commonwealth of Australia, 1996) states in chapter 7 (implementation):

> '*By the year 2000 Australia will have.....*
>
> *(l) arrested and reversed the decline of remnant native vegetation;*
>
> *(m) avoided or limited any further broadscale clearance of native vegetation, consistent with ecologically sustainable management and bioregional planning, to those instances in which regional biological diversity objectives are not compromised;...*'

These actions, signed by the Commonwealth and all the States and Territories, have been addressed through the Natural Heritage Trust (NHT).

The Bushcare program of the NHT aims to influence the States/Territories and local governments (vested with responsibilities by State and Territory legislative frameworks) to achieve ecologically sustainable management of Australia's native vegetation. This will require some change to the current State and Territory legislative and institutional frameworks if it is to be truly effective in halting the decline in the extent and diversity of our natural ecosystems.

The *Intergovernmental Agreement on the Environment* (IGAE, Commonwealth of Australia, 1992a) and the *National Strategy for Ecologically Sustainable Development* (NSESD, Commonwealth of Australia, 1992b) also recognise the importance of the conservation and sustainable use of our natural resources. Both the IGAE and the NSESD provide important benchmarks for the conservation of flora and fauna within the entire landscape matrix. Importantly, both also note the need for the protection and maintenance of native species and habitats outside of strict protected areas.

An important mechanism for providing truly national approaches to the conservation and sustainable use of natural resources has been the Australian and New Zealand Environment and Conservation Council (ANZECC), which is the official council of Ministers of the Environment (previously known as the Council of Nature Conservation Ministers, CONCOM). ANZECC provides a forum for coordinating nature conservation effort. In 1997 ANZECC joined with other natural resource management Ministerial councils in the formation of a Coordinated Working Group on Vegetation.

Local governments also play an important role in flora and fauna conservation. New and innovative schemes are being developed in many shires across Australia, to provide incentives for landowners to conserve flora and fauna on their properties. Such schemes include rate subsidies for involvement of landholders in regional conservation plans and deeds of agreement for assistance in environmental management activities on their land. Many shires are also requiring the retention of native vegetation in particular parts of the landscape, such as along waterways.

The Commonwealth and the States and Territories in concert have also made a number of intra-national commitments to advance the conservation of flora and fauna, including the *National Conservation Strategy* (McMichael, 1982), *Conservation of Species and Ecological Communities Threatened with Extinction* (Australian & New Zealand Environment & Conservation Council, 1997), the *National Strategy for Ecologically Sustainable Development* (Commonwealth of Australia, 1992b), the *National Forest Policy Statement* (Commonwealth of Australia, 1992c), the *Intergovernmental Agreement on the Environment* (Commonwealth of Australia, 1992a), and the *National Strategy for the Conservation of Australia's Biological Diversity* (Commonwealth of Australia, 1996).

Over the past twenty years, and particularly in the last 5 years, the Commonwealth Government has made commitments to a number of international treaties which influence how Australia as a nation deals with protected areas and the conservation of flora. These commitments include the *Apia Convention*, ratified by Australia in 1990; the *Convention for the Protection of the Natural Resources and Environment of the South Pacific Region*, ratified in 1980 (entry into force 1990); the *Convention on the Conservation of Migratory Species of Wild Animals*, ratified by Australia in 1991; the *Convention on Biological Diversity*, ratified by Australia in 1993, the *Framework Convention on Climate Change*, ratified by Australia in 1993, and the *United Nations Commission on Sustainable Development* which meets annually.

While it may seem difficult to link these many and varied commitments to actual advances in flora conservation, there is a very real linkage between government commitments at this highest policy level, and how new protected areas and broader measures for conservation are established. This raft of policies and conventions is the platform on which an integrated effort in protected area establishment is being developed in the nine separate government administrations that have responsibility for both statutory reserves and off-reserve conservation.

A very brief history of conservation reserves in Australia

Over the past one hundred years a great variety of parks and reserves have been declared, gazetted, ungazetted, moved, had bits excised for other purposes, as well as established as important recreational and conservation areas in each State and Territory. It is true to say that while there were many concerned individuals documenting the flora and fauna, there was little government support for conserving land for its own sake between 1788 and the end of the nineteenth century. Generally the white settlers saw Australia as under-populated and under-developed, and the push was for opening areas up for development. Some parks were established within the colonies for recreational purposes, such as Perth Park in the colony of Western Australia (now Kings Park), which was established in 1872 for the purpose of 'public park and recreation' (Rundle, 1996).

The national park movement in the United States in the second half of the nineteenth century saw the establishment of key natural areas (Yellowstone 1872, Adirondacks 1885, Yosemite 1890), for both utilitarian purposes such as water and game supply and for 'people's pleasure' (Nash, 1990). The concept of national parks was taken up within the Australian colonies, and significant parks were set aside in most of the colonies. It is generally conceded that the first Australian national park was Royal National Park just outside of Sydney, gazetted in 1879, and that this park can be regarded as the genesis of our current protected area estate. Thereafter different parks and reserves, mostly selected for scenic value, were gazetted in each colony.

In marked contrast to scenic value as the over-riding criterion for reserve selection, the Australasian Association for the Advancement of Science at its Adelaide meeting in 1893 formalised the concept of establishing reserves for the protection of flora and fauna (Ride, 1975). This followed the passing of the *National Park Act* in South Australia in December 1891, and establishment of that State's first flora and fauna reserve, Belair National Park (Cleland, 1964). In Western Australia the Association put to the government the concept of flora and fauna reserves in diverse areas such as the Abrolhos archipelago and Rottnest Island. While these suggestions were not taken up, a formal reserve for 'Flora and Fauna' was established in South Dandalup, in south-west Western Australia in 1894. The formal *Parks and Reserves Act 1895* was not yet in force in Western Australia, and although concerned scientists and citizens fought for the reserve it was eventually converted to 'Timber-Government Requirements' in 1911 (Rundle, 1996).

Over the past one hundred years there have been numerous government and non-government reports that have called for concerted action to conserve Australia's flora and fauna and, in more recent years, total biological diversity. Several key reports are notable for having influenced informed opinion and hence government action. The Australian Academy of Science (AAS) prepared a series of reports from the AAS State sub-committees on the status of National Parks, culminating in the publication of a report for the whole of Australia, 'National Parks and Reserves in Australia, 1968' (Australian Academy of Science, 1968).

In its 1968 report the Academy provided details of the existing National Parks and Reserves, commented on the adequacy of the current systems of national parks (and reserves), and expressed the need to

> '*ensure that representative environments are available as flora and fauna reserves, that areas of special geological or anthropological interest are not despoiled, and that features of unique scientific interest will still be available for study by future generations*'.

That report highlighted the problems of having separate systems of terrestrial protected areas, not only in terms of the confusion between the varied terminology employed to categorise parks and reserves, but also in the disparity existing in the management of national parks and all other reserves for the protection of flora and fauna. The report identified the need for parks and reserves to provide adequate coverage of fauna and flora habitats and for nature conservation generally. In 1968 the percentage of land in each State devoted to parks and reserves ranged from 0.5% in Western Australia (the largest State in terms of total area) and 0.6% in Queensland (the second largest State in terms of total area) to 4.2% in Tasmania (the smallest State). The Australia-wide average was 1.2%.

In the late 1960s two separate series of conferences of government Ministers responsible for national parks and wildlife conservation was begun. In 1974 the two groups were merged and the Council of Nature Conservation Ministers was established to report annually on developments in national parks and/or wildlife conservation. Concurrently public interest in the issue of nature conservation was rapidly evolving. Protected Area management and wildlife management became a significant government activity and most jurisdictions updated their legislation to reflect the increase in activities.

The 1960s and 1970s saw the establishment of dedicated parks/wildlife agencies in each State and Territory, building on fauna protection bodies and parks bodies which dated from the turn of the century. Over the last 30 years these agencies have grown to encompass more and more nature conservation issues, including the conservation of all biological diversity.

The Australian Academy of Science instigated several projects during the 1960s that themselves had significant influence on, and indeed continue to influence, our understanding of the need for a national system of protected areas. One such study (Specht *et al*., 1974) can be considered the first national evaluation of the conservation status of the major plant communities of Australia. In that report Specht noted that:

> '*if effective action is to be taken with the conservation of the primitive, rare or endangered plants in Australia the following steps appear to be necessary:*
>
> *(1) to record the present distribution of all plant species; to record their presence in existing parks and reserves; if these reserves are placed in categories lower than providing the best conditions for their conservation, there will be a strong argument in*

> *favour of upgrading the reserve to provide maximum protection; to monitor the protected populations to ensure their continued survival. Very little is known of the biology and ecology of most of the plants and steps should be taken to fill the gaps in our knowledge. Some should be brought into cultivation in Botanical gardens.*'

Also in 1974 the Academy held a conference under the auspices of the International Biological Programme which recommended that at least one reasonably large sample of each major ecosystem in each biogeographical division of each State should be incorporated into an 'ecological reserve', either by designating the whole or part of existing national parks and other nature conservation reserves as ecological reserves, or, where necessary, by acquisition of land (Fenner, 1975).

The growth in public interest and activity in nature conservation matters was perhaps greatest in the 1970s. Hydroelectric dams, timber harvesting, mining, and general concern over inadequate protection for flora and fauna became national issues. The Commonwealth Parliament appointed an Inquiry into Wildlife Conservation in 1972 to investigate the commercial exploitation of native wildlife (particularly kangaroos), nature conservation survey methods, the adequacy of reserve systems, and mechanisms to ensure better conservation management (House of Representatives Select Committee, 1972). Flowing from the recommendations of that Inquiry was the establishment of the Australian National Parks and Wildlife Service (ANPWS) in 1975 and the Great Barrier Reef Marine Park Authority (GBRMPA) in 1976.

Another Commonwealth Government initiative of that time was the Committee of Inquiry into the National Estate to investigate the identification and conservation of Australia's cultural and natural heritage of national and international significance (Committee of Inquiry into the National Estate, 1974). The Commonwealth passed the *States Grants (Nature Conservation) Act 1974* to provide financial assistance to the States for nature conservation programs, which was used for a short period in the late 1970s to assist the States with the acquisition of new parks and reserves.

An important initiative of the 1970s was the establishment of the Australian Man and the Biosphere Committee, which helped in the setting up of Australia's first Biosphere Reserves. Between 1976 and 1982 twelve Biosphere Reserves were designated (they were already protected areas under State or Commonwealth legislation) recognising the international significance of these areas from the perspective of their characteristic plants, animals and human usage. More recently biosphere reserves are being viewed as containing a gradation of human usage and modification, from core conservation zones, to buffer zones allowing human activities compatible with the conservation activities, and finally to outer transition zones which allow the practice of sustainable development. Australian biosphere reserves will inevitably change in accordance with these new developments in bioregional planning.

In the 1980s and 1990s many jurisdictions have chosen to merge parks/wildlife services into larger government departments dealing with natural resource management. The growth in the complexity of our government structures dealing with nature conservation reflects the growth in public concern over environmental issues.

In the 1970s some States began systematic evaluation of the protected area estate, and programs to acquire additional land for parks were initiated. The Land Conservation Council in Victoria and the Conservation through Reserves Committee in Western Australia are two examples of government appointed bodies set up to make recommendations for the establishment of a representative reserve system in those States.

Between 1968 and 1978 the area of terrestrial parks and reserves in Australia almost doubled. Western Australia exhibited the largest increase from 0.5% in 1968 to 5.0% in 1978. Overall Tasmania continued to have the largest percentage of its area in protected areas increasing from 4.2% in 1968 to 10% of the State in 1978 (Bridgewater & Shaughnessy, 1994).

Australia became a party to the *World Heritage Convention* in 1974, but the first Australian sites were not accepted for inscription on the World Heritage List until 1981. (Currently there are 11 properties listed for their natural heritage values and some are also listed for their cultural heritage values, and one is a cultural landscape. While most world heritage sites have been declared over existing protected areas, several world heritage areas are made up of a mix of tenures, e.g. Willandra Lakes and the Wet Tropics).

The concept of World Heritage had a marked effect in the 1980s on public reaction to development proposals, and subsequently in government action. The issue which generated the greatest public concern was the plan of the Tasmanian Government to build a major hydroelectric dam within the Tasmanian World Heritage Area. Effective campaigns by non-government conservation organisations placed intense pressure on the Commonwealth to take action to prevent the dam from being built, on the premise that although the site was under Tasmanian jurisdiction, the Commonwealth was obliged to intervene because of its ultimate responsibility for implementation of international treaties (Bridgewater & Shaughnessy, 1994). The issue became nationally important in the run-up to the 1983 federal election, with the then Labor Opposition promising action to halt the dam if elected, in what was for Australia the first time a conservation issue was a major election issue. The Labor Opposition won office and was held to its promises by vocal conservation groups. The Tasmanian Government, however, was adamant the dam should go ahead.

The result of this impasse saw the Commonwealth Parliament enact the *World Heritage Properties Conservation Act 1983* which provided the Commonwealth with the power to prohibit actions which might damage or destroy a World Heritage site, and it used that power to prohibit construction of the dam (Bridgewater & Shaughnessy, 1994). The use of this new Commonwealth power in relation to the *World Heritage Convention* encouraged non-government conservation organisations subsequently to seek World Heritage Listing as a protective mechanism for significant sites which were considered inadequately protected by State governments. This approach resulted in the listing of the wet tropical rainforests of Queensland in 1988 and a major expansion of the Tasmanian World Heritage Area in 1989, with concomitant cessation of forestry activities in both areas (Bridgewater & Shaughnessy, 1994).

During the 1970s and 1980s the significance of marine protected areas for conservation became a prominent issue, taken up by non-government groups and governments. The largest marine park in the world, the Great Barrier Reef Marine Park (GBRMP), covering 34.5 million ha, was established in 1975. The GBRMP was drawn up with management zones to allow multiple-use of certain areas while still ensuring the protection of the Reef. Zoning plans were created to allow for uses such as diving, reef-walking, recreational and commercial fishing and for general tourist activities.

Other marine areas were also established in other parts of Australia though not on the scale of the Great Barrier Reef Marine Park. A report prepared by the State and Commonwealth Environment Ministers in 1979 concluded that there was strong justification for the establishment of a system of marine parks and reserves in Australia (Ivanovici, 1984).

In the 1980s a new term was coined to encompass all known living organisms: 'biodiversity'. Biodiversity has become part of the political lexicon, and its conservation has gained far greater recognition as a fundamental component of maintaining the ecological processes upon which we depend. In Australia we have seen a massive increase in effort in both on and off reserve conservation. The rate of discovery (publication) of new species has also increased markedly, and yet the estimates of the number of unknown species continues to grow, particularly for invertebrates and fungi. Orchard (*pers. comm.*) has shown that for vascular plants the average rate of description of new taxa has averaged 90 species a year from 1788 until 1990, and that the rate has been fairly constant. However, in recent years the rate has increased, and in the period 1990–1996 has been estimated at an average of about 140–150 species per year (range 86–316 per year) (Orchard & Briggs, *pers. comm.*). For the same period about 30 mosses, lichens and algae were described per year. Orchard (1998, this volume) has suggested that the total known vascular flora for Australia at the time of completion of the first edition of *Flora of Australia* (c. 2015) will probably stand at just over 20 000 species, including naturalised taxa.

The need for a representative system of protected areas in Australia was recognised in two inquiries by a bipartisan Commonwealth parliamentary committee, the House of Representatives Standing Committee on Environment, Recreation and the Arts (HoRSCERA) in 1992. The reports from that committee recommended that a bioregional approach be developed and adopted as a key element of a unified methodology for identifying and prioritising establishment of new reserves in areas currently under-represented (HoRSCERA, 1992; Brunckhorst, 1992, 1993). The then Prime Minister, Paul Keating, announced a new federal program to coordinate the development of a national reserve system (NRS) using such an approach (Keating, 1992). The NRS program was established with the aim of developing and implementing the national system of protected areas in Australia in cooperation with the States and Territories.

The current system of protected areas

Each of the nine jurisdictions (the Commonwealth, six States and two self-governing Territories) has its own government agency with responsibility for management of that jurisdiction's protected areas and, indeed, nature conservation more broadly. Apart from those lead agencies (often the National Parks and Wildlife Service) there are a range of other agencies, responsible for forestry, fisheries, and/or regional management, that have legislative responsibilities for protected areas which help conserve biodiversity.

While in the past the acquisition of protected areas has not been carried out on a systematic basis to optimally conserve biodiversity, all nature conservation agencies in Australia now have a formal commitment to the establishment of a protected area system which represents all major ecosystems within their area of jurisdiction. *The National Strategy for the Conservation of Australia's Biological Diversity*, signed by all governments has as an explicit objective to

> '*Establish and manage a comprehensive, adequate and representative system of protected areas covering Australia's biological diversity*' (Commonwealth of Australia, 1996).

The Australian Government instigated the largest ever Australian environment program, the Natural Heritage Trust (NHT) in 1996, to implement a wide range of conservation programs to foster the long term protection of all biodiversity, including flora. The NHT has a major protected area extablishment program which will help redress inadequacies in the current protected area system.

A detailed listing of each jurisdiction's legislation and protection measures for the conservation of flora, particularly in relation to protected areas

Commonwealth

The *National Parks and Wildlife Conservation Act 1975* provides for the establishment of parks and reserves over areas of land or sea where constitutionally there is a basis for Commonwealth interest. These areas may be named as a national park or other designation and may only be revoked by a resolution of each House of Parliament. Plans of management must be prepared and subjected to public comment and scrutiny by both Houses of Parliament. Parks and reserves have been declared under the Act in the Northern Territory, the Jervis Bay Territory, the Australian Capital Territory, in five external territories and in Commonwealth waters over the Australian continental shelf. The Norfolk Island National Park and Botanic Garden are declared under both the National Parks and Wildlife Conservation Act and under legislation of the Norfolk Island Legislative Assembly.

The *National Parks and Wildlife Conservation Act 1975* has been amended several times to include joint management provisions to apply to Uluṟu Kata-Tjuṯa, Kakadu and Booderee National Parks. These National Parks are on land fully or mostly owned by Aboriginal people and leased back to the Director of National Parks and Wildlife. Aboriginal people have a majority on the Boards of Management. Regulations under the *National Parks and Wildlife*

Conservation Act 1975 also protect certain species in areas under Commonwealth jurisdiction, including the Economic Exclusion Zone, outside of designated protected areas.

The *Great Barrier Reef Marine Park Act 1975* provides for the conservation of the Great Barrier Reef by the establishment, control, care, and development of the Great Barrier Reef Marine Park (GBRMP). Declaration of areas as part of the GBRMP may only be revoked by a resolution passed by each House of Parliament. The Act requires the preparation of zoning plans for the Marine Park which, after being subject to public comment and amendment, are considered by the responsible Minister and laid before both Houses of Parliament. Human use is controlled mainly by regulation and by the development of zoning plans. Mining and oil exploration are prohibited in the Marine Park.

Under the *Antarctic Treaty (Environment Protection) Act 1980* the Governor-General may proclaim an area in Antarctica to be a specially protected area or a site of special scientific interest, in accordance with designations made under the Antarctic Treaty. The Act provides for the Minister to grant permits authorising entry into, and conduct of certain activities within, those areas.

Article 2 of the Madrid Protocol on Environmental Protection to the Antarctic Treaty, which was adopted in October 1991, designates Antarctica as a natural reserve devoted to peace and science. Among other things, the protocol prohibits activity relating to mineral resources other than scientific research. Annex V of the Protocol rationalises the Antarctic protected area system, providing for two principal categories, Antarctic Specially Protected Areas and Antarctic Specially Managed Areas, and a third category of Historic Sites and Monuments. The Madrid Protocol came into force in February 1998, with the exception of Annexe V which several Treaty parties have yet to ratify. Newly designated protected areas will be consistent with the requirements of Annexe V.

The Territory of Heard Island and the McDonald Islands is established under the *Heard Island and McDonald Islands Act 1953*. The *Environment Protection and Management Ordinance 1987*, made under the Act, provides for the protection of the environment and indigenous wildlife of the Territory. Among other things, it provides for a permit system for all entry to, and activities within, the Territory, and it requires a management plan to be prepared. The Heard Island Wilderness Reserve Management Plan came into operation in February 1996, and the Islands were inscribed on the World Heritage list in 1996.

Australia's other subantarctic territory, Macquarie Island, however, comes under the jurisdiction of the Tasmanian State Government, and is administered by that State's Parks & Wildlife Service (*q.v.*). It was inscribed on the World Heritage list in 1997.

The *Environment Protection (Alligator Rivers Region) Act 1978* established the Office of the Supervising Scientist to ensure protection of the environment of the Alligator Rivers region from any adverse effects of uranium mining.

The *Endangered Species Protection Act 1992* provides for national action to promote the recovery of listed endangered or vulnerable species and listed endangered ecological communities, and controls the actions of Commonwealth agencies and activities on Commonwealth property that may impact on them. It also prescribes key threatening processes which impact on endangered species and requires their management through recovery plans and threat abatement plans. These activities are designed to ensure integrated conservation efforts across Australia, with the Commonwealth providing State and Territory agencies with additional funding to implement these recovery and threat abatement plans for threatened flora and fauna on both public and private lands.

The *Wet Tropics of Queensland World Heritage Area Conservation Act 1994* provides for the implementation of Australia's international obligations under the World Heritage Convention in relation to the Wet Tropics area of Queensland. It reflects an agreement made between the Queensland and Commonwealth governments in 1990 to protect, conserve, and rehabilitate the remaining rainforest areas in the 'wet tropics'.

Several historic shipwrecks in waters under Commonwealth jurisdiction have had 'protected zones' designated around them under the *Historic Shipwrecks Act 1976.* While these areas are declared primarily to protect the enclosed shipwrecks, the legislation prohibits entry or mooring of ships, trawling, diving, or any other activity, effectively protecting all marine life in the designated area. A permit is required to enter the area for any purpose. Other shipwrecks have also been declared historic under the Act. Interference with these wreck sites or the removal of any parts or articles from these wrecks is prohibited without a permit. However, access which does not cause disturbance is unrestricted.

On 1 April 1993 all shipwrecks and associated relics 75 years old or older were declared historic under the Act in what is known as the Blanket Declaration and are now subject to the provisions of the Act. Younger shipwrecks of historic significance are still declared historic under Section 5 of the Act.

As this book was going to press a new Bill, the *Commonwealth Environment Protection and Biodiversity Conservation Bill*, was being considered by the Federal Parliament. This Bill, if passed, would amalgamate the *National Parks and Wildlife Conservation Act 1975*, parts of the *National Parks and Wildlife Regulations*, *Endangered Species Protection Act 1992*, *Whale Protection Act 1980*, *World Heritage Properties Conservation Act 1983*, and *Environment Protection (Impact of Proposals) Act 1974*, into one piece of legislation. The Bill would also provide legislative frameworks for identification and monitoring of components of biodiversity, protection for Ramsar wetlands and Biosphere reserves, conservation of listed migratory species, and access to biological resources.

Australian Capital Territory

The *Nature Conservation Act 1980* provides for the conservation of native flora and fauna and gives management authority for protected areas (nature reserves, national parks and wilderness zones). Native vegetation is protected on all unleased land.

Currently (as at September 1998) the Australian Capital Territory has one National Park covering an area of 105 800 ha (including a 28 900 ha wilderness zone), one Landscape Conservation Reserve (IUCN category V) of 1300 ha, and 33 Nature Reserves (IUCN Category II) ranging from less than 10 ha to 4500 ha and covering a total area of 16 800 ha.

A 1994 amendment to the Act established a process for identification, declaration and protection of threatened species and ecological communities. As of August 1998, five plant species and two ecological communities have been declared.

The *Land (Planning and Environment) Act* 1991 establishes the Territory Plan, which is the statutory vehicle for reserving public land and for determining land use constraints generally. Management objectives for protected areas are prescribed in terms of conservation and public use priorities. The Act also provides for the identification and protection of natural heritage places. Over 50% of the Australian Capital Territory is reserved for conservation of the natural environment.

The management of protected areas, and other public lands where conservation of natural and cultural heritage is a primary management objective, is undertaken by the ACT Parks and Conservation Service on behalf of Environment ACT, the Government's environmental conservation agency.

The Environment Advisory Committee is the primary forum for advice to the Government on environmental matters. The Flora and Fauna Committee has a statutory role in formal identification of species and communities at risk of extinction and the provision of associated expert advice.

Off reserve conservation of native flora on occupied (leased) land is primarily addressed through lease administration mechanisms. The development of Property Management Agreements as an attachment to a rural lease is a relatively new initiative that provides for the identification of nature conservation values on the land and implementation of appropriate management measures. A financial incentive mechanism for landholders is under development. Particular attention is being paid to the conservation requirements of remnant vegetation generally and threatened woodland and grassland communities in particular.

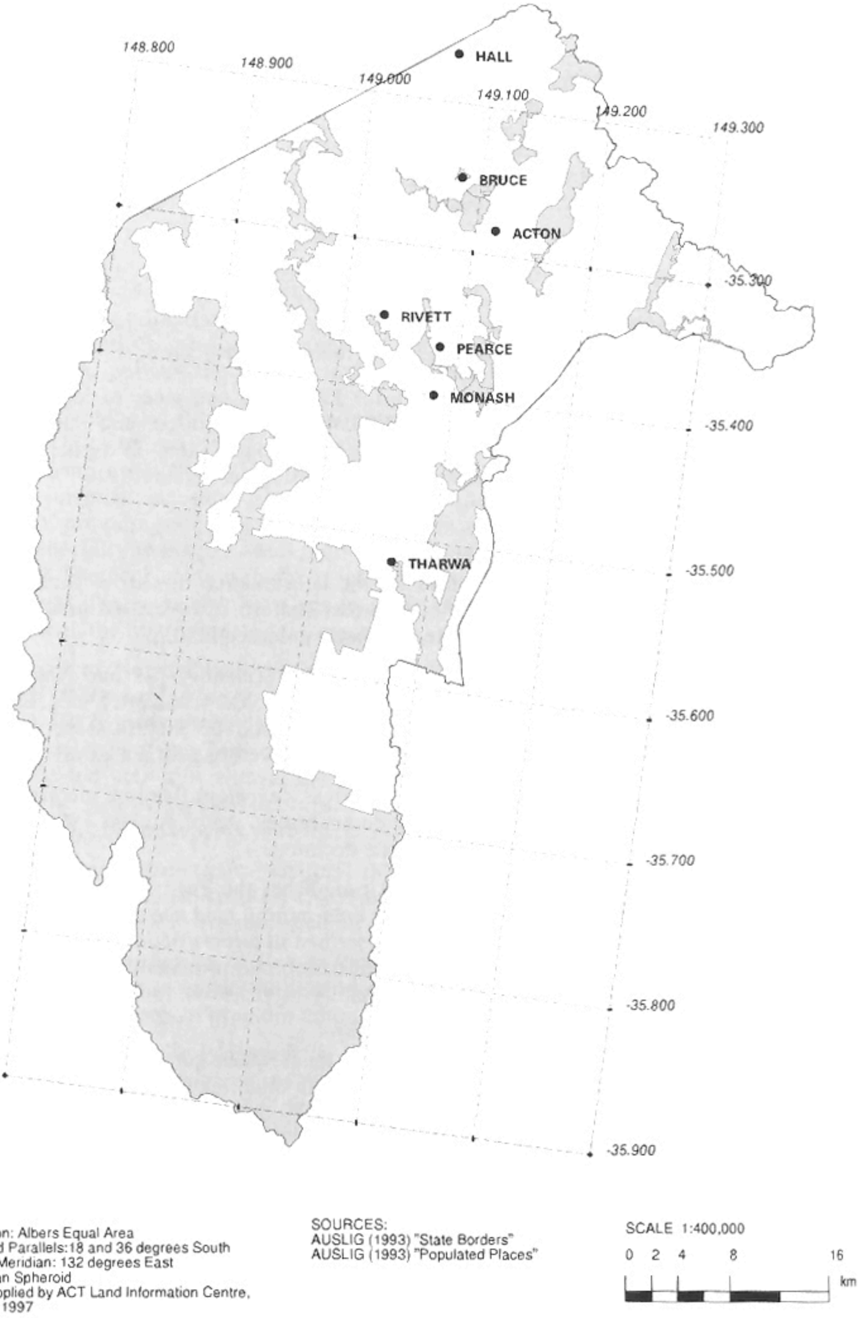

148.800
148.900
149.000
149.100
149.200
149.300
HALL
BRUCE
ACTON
RIVETT
PEARCE
MONASH
THARWA
-35.300
-35.400
-35.500
-35.600
-35.700
-35.800
-35.900
Projection: Albers Equal Area
Standard Parallels:18 and 36 degrees South
Central Meridian: 132 degrees East
Australian Spheroid
Data supplied by ACT Land Information Centre, January 1997
SOURCES:
AUSLIG (1993) "State Borders"
AUSLIG (1993) "Populated Places"
SCALE 1:400,000
0 2 4 8 16
km

Figure 91. Terrestrial protected areas of the Australian Capital Territory. Source: I.D.Cresswell and G.M.Thomas (1997), *Terrestrial and Marine Protected Areas in Australia*. Environment Australia Biodiversity Group, Canberra. Reproduced with permission.

New South Wales

The *National Parks and Wildlife Act 1974* provides for the creation and management of National Parks, Historic Sites, Nature Reserves, Aboriginal Areas, State Game Reserves, Karst Conservation Reserves and State Recreation Areas. The *Wilderness Act 1987* provides for the investigation, identification, protection and management of wilderness in New South Wales.

Currently (as at 7 October 1998) New South Wales has 104 National Parks covering an area of 3 774 980 ha, 217 Nature Reserves covering an area of 643 456 ha, ten Aboriginal Areas covering an area of 11 521 ha, six Regional Parks covering an area of 4611 ha, 167 Flora Reserves covering an area of 47 656 ha, 18 State Recreation Areas covering an area of 122 113 ha, and 13 Historical Sites covering an area of 2615 ha.

Plans of management are prepared for all of these areas having regard to the objectives of conservation, study and appreciation of wildlife and natural and cultural features, and to promote appreciation and enjoyment of the natural and cultural values of the areas. They are subject to public comment before adoption by the Minister for the Environment.

The Act establishes a National Parks and Wildlife Advisory Council to advise the Minister on the control and management of national parks and nature reserves. Advisory committees may also be established for one or more national parks, nature reserves and historic sites or any combination thereof, to make recommendations to the Council, the Director of the National Parks and Wildlife Service, or the District Manager of the respective National Park.

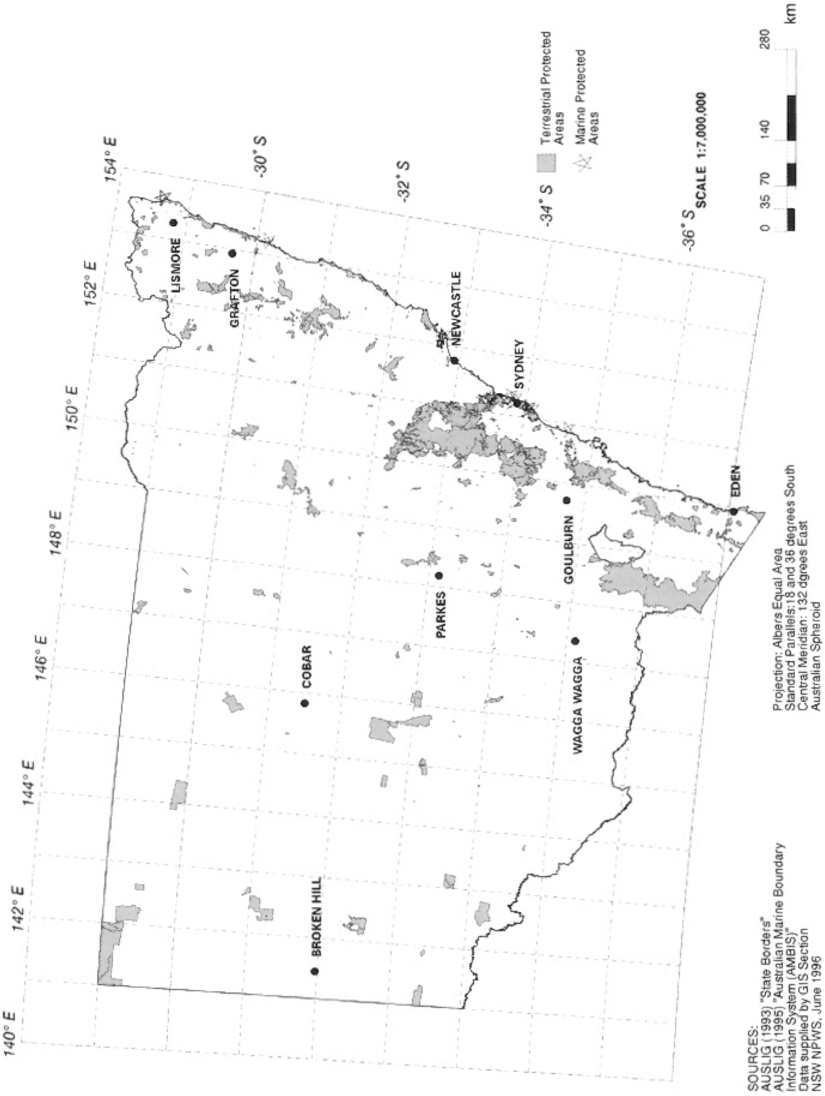
'Conservation Agreements', a voluntary scheme set up under the *National Parks and Wildlife Act 1974*, commenced in 1986 and operates on Crown lease and freehold land to promote the conservation of natural and cultural heritage on land outside reserves. These Agreements are binding on successors to the title and may provide financial or other assistance to the landholder.

National Parks, Nature Reserves, State Recreation Areas, Historic Sites, Wilderness Areas and Aboriginal Areas are managed by the New South Wales National Parks and Wildlife Service, which was established under the *National Parks and Wildlife Act 1974*. The Service is responsible to the Minister for the Environment.

The *Forestry Act 1916*, provides that land within State Forest and certain Crown lands may be dedicated, by notice in the *Government Gazette*, as a Flora Reserve for the preservation of native flora. To date all such reserves have been located within State Forest (Flora Reserves are managed by New South Wales State Forests), and while the preservation of native flora remains the keystone for all Flora Reserves, establishment and management of the reserves have always been based on a broader objective of preserving samples of the natural environment. A Flora Reserve can only be revoked by Act of Parliament, and for each reserve New South Wales State Forests is required to prepare a working plan for approval by the Minister for Land and Water Conservation and Forests. For a number of Flora Reserves which receive appreciable public use, advisory committees have been set up under the working plans to assist in the care of the reserves.

The *Soil Conservation Act 1938* establishes the Soil Conservation Service to arrest land degradation, and allows for the declaration of 'protected land' where trees may not be destroyed without authority. Under the Act, environmentally sensitive land or land liable to be affected by degradation, land with a slope greater than 18º and land within 20 metres of a river or lake, are 'protected lands'. Environmentally sensitive land includes arid areas, landslip or saline areas and land containing rare or endangered wildlife, sites of archaeological or historic interest, bird breeding grounds, wetlands or areas of scenic beauty.

A clearing licence cannot be issued under the *Forestry Act 1916* in respect of protected land, without the consent of the Catchment Areas Protection Board. When authority has been given to destroy timber on protected lands, conditions may be imposed to prevent a wide range of activities that may cause degradation. Soil Conservation Orders may be issued which require land holders to carry out specific works on protected land or erosion hazard areas.



SOURCES:
AUSLIG (1993) "State Borders"
AUSLIG (1995) "Australian Marine Boundary
Information System (AMBIS)"
Data supplied by GIS Section
NSW NPWS, June 1996

Projection: Albers Equal Area
Standard Parallels:18 and 36 degrees South
Central Meridian: 132 dgrees East
Australian Spheroid

Figure 92. Terrestrial protected areas of the Australian Capital Territory.
Source: I.D.Cresswell and G.M.Thomas (1997), *Terrestrial and Marine Protected Areas in Australia*. Environment Australia Biodiversity Group, Canberra. Reproduced with permission.

The *Fisheries Management Act 1994*, and previously the *Fisheries and Oyster Farms (Amendment) Act 1979* provides for the creation and management of Aquatic Reserves in New South Wales. At present, the legislation specifies that Aquatic Reserves may only be declared over areas designated as 'Crown lands', and that the regulations may prohibit or regulate the taking of fish and other aquatic fauna as specified in the Act. In relation to the conservation of flora the regulations also provide for the management, protection and development of Aquatic Reserves. These are managed by New South Wales Fisheries, on behalf of the Minister for Mineral Resources and Fisheries.

Marine Parks are jointly gazetted by the Minister for Fisheries and the Minister for the Environment under the *Marine Parks Act 1997*. The first two marine parks established in New South Wales were Jervis Bay Marine Park and Solitary Island Marine Park, declared on 29 December 1997. Marine Parks are managed by the Marine Parks Authority, comprising the Director of New South Wales Fisheries, the Director General of the National Parks and Wildlife Service, and the Director General of the Premier's Department.

The *Lord Howe Island Act 1953* makes special provision for the management and protection of Lord Howe Island, applying the provisions of the *National Parks and Wildlife Act 1974,* and dedicates some 75% of the island and all the surrounding islands as the Lord Howe Island Permanent Park Preserve. Control of the Lord Howe Island Permanent Park Preserve is vested in the Lord Howe Island Board. Lord Howe Island was inscribed on the World Heritage list in 1982.

The *Environmental Planning and Assessment Act 1979* provides for the zoning of land under local and regional plans and State Environment Protection Policies to protect sensitive areas, particularly making provision for the protection and preservation of trees or vegetation, and requires a consent authority (for example a local government) to take into account the preservation of trees and vegetation in determining a development application (as well as many other environmental values such as air and water quality). If vegetation or trees are damaged or removed without authority, then the person who is guilty may have to plant new trees and maintain them to full growth. If a development does not need consent under the *Environmental Planning and Assessment Act 1979,* the *Local Government Act 1919* requires tree preservation to be considered where building or subdivision is to take place.

The *Coastal Protection Act 1979* established the Coastal Council of New South Wales which advises, and provides recommendations, on the protection and conservation of the coastal zone.

The *Crown Lands Act 1989* provides for the management of Crown Lands for the benefit of the people of New South Wales, particularly to ensure the conservation of the environment (water, soil, flora and fauna) and the scenic qualities of the land. While the Act does provide for controls on clearance of native vegetation on leasehold land, in effect it has been rarely enforced since the 1970s (University of Melbourne School of Forestry, 1994).

The *Protection of the Environment Administration Act 1991* established the Environment Protection Authority which acts to reduce pollution and degradation of the environment.

The *Threatened Species Conservation Act 1995* provides for the conservation of threatened species, populations and ecological communities, and prescribes key threatening processes which impact on endangered species and requires their management through the implementation of recovery plans, threat abatement plans and other conservation measures. The *Threatened Species Conservation Act 1995* sets up a statewide system to protect species (plant and animal), populations and ecological communities and to monitor key threatening processes. It incorporates regulation of these matters into the planning process and provides for the preparation by the National Parks and Wildlife Service of recovery plans for threatened species, populations and ecological communities.

The New South Wales Government *State Environmental Planning Policy No 46* 'Protection and Management of Native Vegetation' (known as SEPP 46) was established in 1995. In August 1995 the Native Vegetation Forum was set up to review the performance of SEPP 46, and to provide recommendations concerning the reform of vegetation management in the

State. As a result the New South Wales Government has put in place a new package of measures on native vegetation.

The New South Wales Native Vegetation Package consists of four main elements:

- Legislation. The New South Wales Government has enacted the *Native Vegetation Conservation Act 1998* to replace SEPP 46 in relation to land clearing approvals, the preparation of Regional Vegetation Management Plans, the operation of an incentives fund and the proposed State Vegetation Advisory Council;
- Regional Vegetation Management Plans. Regional vegetation committees will be set up to develop these plans. When plans are approved by the Minister the landholder can carry out native vegetation clearing within the limits of the plan without the need for additional site-specific approval;
- Native Vegetation Management Fund ($15 million over 5 years). Landholders who enter into a 'Property Agreement' with the New South Wales Government dealing with vegetation management will be eligible for support from the fund. The fund focuses on
    - protection of remnant native vegetation of high conservation value
    - maintenance and enhancement of existing native vegetation, and
    - revegetation.
- Native Vegetation Advisory Council. This Council will advise the New South Wales Government including
    - the development and review of strategic native vegetation policy
    - the review of Regional Vegetation Management Plans, and
    - a statewide audit, review and annual reporting of native vegetation conservation and identification of priorities for incentives.

Northern Territory

The *Parks and Wildlife Commission Act 1980,* as amended in 1995, established the Parks and Wildlife Commission of the Northern Territory (PWCNT) to promote the conservation and protection of the natural environment of the Northern Territory. The Commission achieves this objective by establishing and managing parks, reserves and sanctuaries, as well as managing Aboriginal and other privately owned land by agreement with the landholder. The Commission is a corporation of at least nine members, including the Director of the Commission, the Chief Executive Officer of the Northern Territory Tourist Commission, at least three Aboriginals (nominated by Land Councils or other Aboriginal organisations) and at least two members with scientific expertise.

The *Territory Parks and Wildlife Conservation Act 1977,* as amended 1992, provides for the declaration of Parks, Reserves, Sanctuaries and Protected Areas both on land and in the sea above any part of the seabed of the Territory. The Administrator of the Northern Territory may declare a park/reserve following the receipt of a report from the Parks and Wildlife Commission. Areas declared may range from small sites of specific interest to major national parks. Land is held by the Conservation Land Corporation constituted under the *Parks and Wildlife Commission Act 1995*. Revocation of a park/reserve may only be declared by the Administrator in accordance with a resolution passed by the Legislative Assembly.

Currently (as of October 1998) the Northern Territory has nine National Parks covering an area of 1 996 833 ha, four 'Aboriginal Lands managed as National Parks' covering an area of 582 649 ha, 15 Conservation Areas covering an area of 143 168 ha, 15 Conservation Reserves covering an area of 43 044 ha, 14 Nature Parks covering an area of 24 587 ha, 15 Historic Reserves covering an area of 11 293 ha, and 18 'Other Protected Areas' covering an area of 153 208 ha.

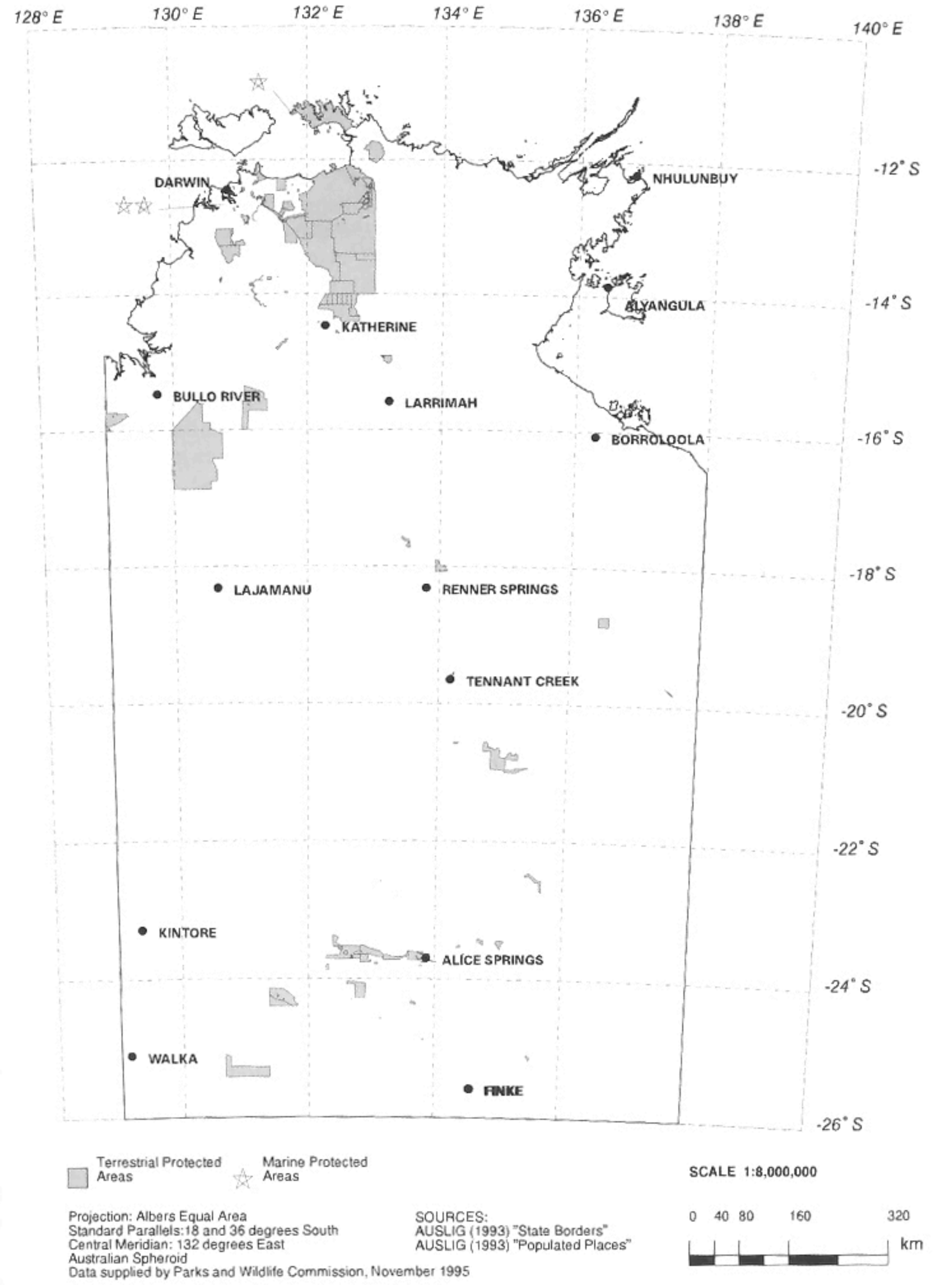


Figure 93. Terrestrial and marine protected areas of the Northern Territory. Source: I.D.Cresswell and G.M.Thomas (1997), *Terrestrial and Marine Protected Areas in Australia*. Environment Australia Biodiversity Group, Canberra. Reproduced with permission.

Management plans are prepared by the Parks and Wildlife Commission of the Northern Territory for areas under its control in accordance with the *Territory Parks and Wildlife Conservation Act 1977*.

The Gurig National Park, located on the Cobourg Peninsula, was established in 1981, and amended in 1996 by the *Cobourg Peninsula Aboriginal Land, Sanctuary and Marine Park Act 1996*. The land is owned by Aboriginal traditional owners and is leased to the Parks and Wildlife Commission of the Northern Territory. The park is managed by the Commission pursuant to direction of the Cobourg Peninsula Sanctuary and Marine Park Board. The Board consists of eight members, four of whom are Aboriginals nominated by the Land Councils.

The Nitmiluk (Katherine Gorge) National Park was established in a similar manner pursuant to the *Nitmiluk (Katherine Gorge) National Park Act 1989*. Again, the park is managed by the Commission on advice from a Board. Of the 13 members of the Board, eight are traditional Aboriginal owners of the Park nominated by the Jawoyn Association, four are members of the permanent staff of the Commission and one is a resident of the Katherine area nominated by the Mayor of Katherine.

Under the *Crown Lands Act 1992*, ownership of all flora on Crown land (10% of the Territory) and Crown leasehold land (50% of the Territory) is vested with the Northern Territory Government. Any commercial activity involving destruction of vegetation must be licensed by the Parks and Wildlife Commission. Also under the *Crown Lands Act 1992*, where an application has been received for a perpetual pastoral lease, it is inspected to determine whether any areas should be reserved for public interest including conservation values. Any subsequent lease issued may be subject to conditions.

The *Pastoral Land Act 1992* requires pastoral leases to obtain the written consent of the Northern Territory Pastoral Land Board prior to undertaking clearing, except where clearing is for roads/tracks, firebreaks, yards or watering points. It is understood that, in practice, this consent is rarely withheld.

Queensland

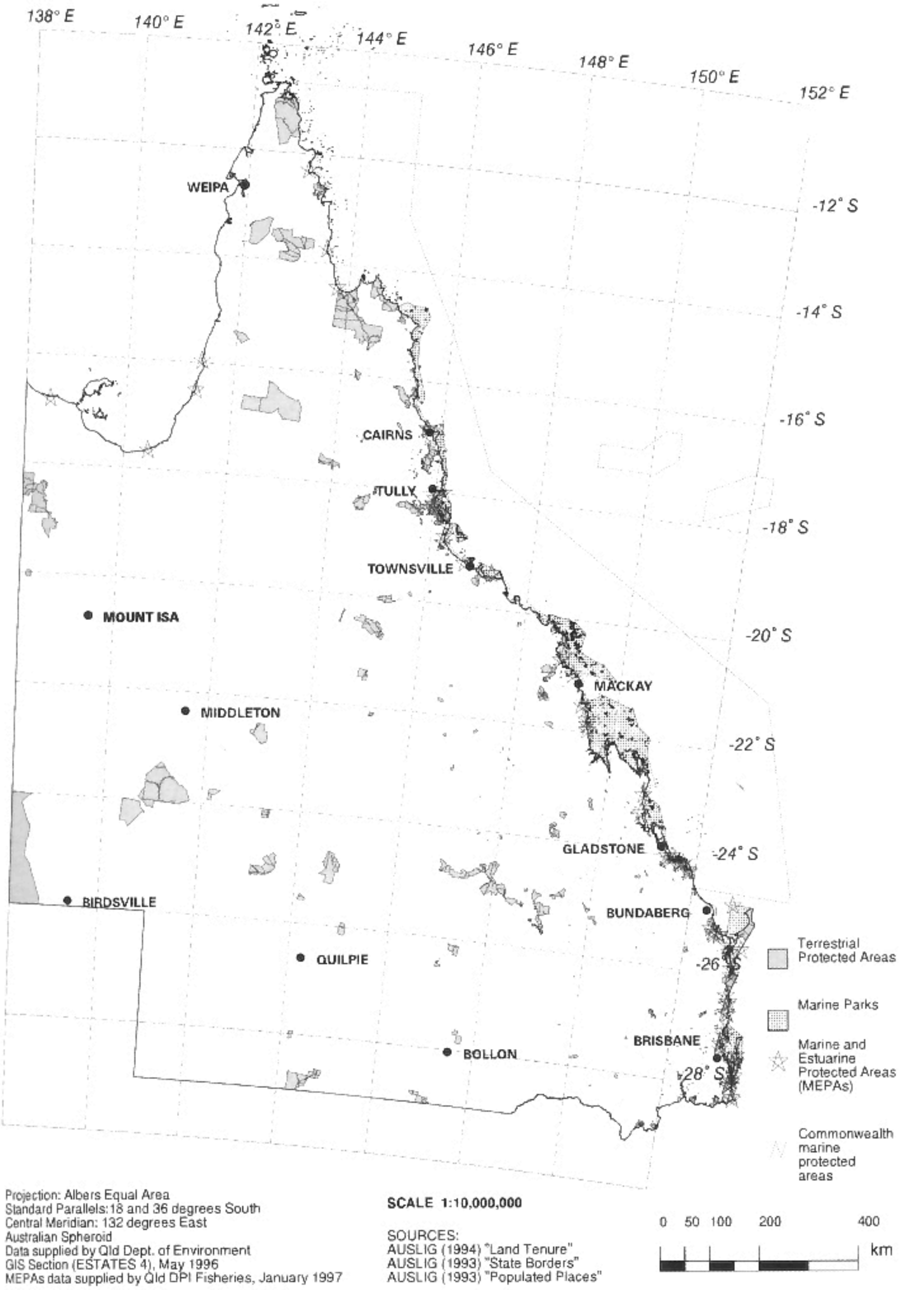
The *Nature Conservation Act 1992* provides for the dedication and declaration of eleven classes of protected area. These are:

- Protected areas that can be declared over State land; these include: National Park (Scientific), National Park, Conservation Park, and Resources Reserve.
- Protected areas that can be declared over Aboriginal or Torres Strait Islander land leased to the Crown, or over leasehold land subleased to the Crown; these include: National Park (Aboriginal Land), and National Park (Torres Strait Islander Land).
- Protected areas that can be declared over State land or private land: these include: Nature Refuge, Coordinated Conservation Area, Wilderness Area, World Heritage Management Area, and International Agreement Area.

The Department of Environment and Heritage is responsible for environmental management and conservation of Queensland's natural and cultural resources. The *Nature Conservation Act 1992* and the *Marine Parks Act 1982* are administered by the chief executive of the Department, subject to the Minister for Environment and Heritage.

Currently (as at 4 September 1998) Queensland has seven National Parks (Scientific) and 213 National Parks covering an area of 6 605 062 ha, 159 Conservation Parks covering an area of 29 066 ha, and 39 Resource Reserves covering an area of 344 645 ha.

A management plan must be prepared for each protected area or aggregation of protected areas, but a nature refuge may be exempted in the conservation agreement between the Minister and the landholder(s). A protected area must be managed in accordance with an approved management plan, and regulations may be made to give effect to, or enforce compliance with, an approved plan.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WEIPA
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TULLY
TOWNSVILLE
MOUNT ISA
MACKAY
MIDDLETON
GLADSTONE
BIRDSVILLE
BUNDABERG
QUILPIE
BRISBANE
BOLLON
Terrestrial Protected Areas
Marine Parks
Marine and Estuarine Protected Areas (MEPAs)
Commonwealth marine protected areas
Projection: Albers Equal Area
Standard Parallels: 18 and 36 degrees South
Central Meridian: 132 degrees East
Australian Spheroid
Data supplied by Qld Dept. of Environment
GIS Section (ESTATES 4), May 1996
MEPAs data supplied by Qld DPI Fisheries, January 1997
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SOURCES:
AUSLIG (1994) "Land Tenure"
AUSLIG (1993) "State Borders"
AUSLIG (1993) "Populated Places"
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Figure 94. Terrestrial and marine protected areas of Queensland. Source: I.D.Cresswell and G.M.Thomas (1997), *Terrestrial and Marine Protected Areas in Australia*. Environment Australia Biodiversity Group, Canberra. Reproduced with permission.

The *Land Act 1994* provides for the establishment of a range of tenures for community purposes related to environmental, natural resource management and scientific purposes. Unallocated State land may either be granted in fee simple in trust for these purposes or dedicated as a reserve.

The Department of Natural Resources is responsible for the management of State Forests under the *Forestry Act 1959,* as amended 1987. Section 33 of the *Forestry Act 1959* sets out the cardinal principles of management of State Forests as

> '*permanent reservation, production of timber and associated products in perpetuity, and protection of watersheds, having due regard to: the benefits of permitting grazing, the desirability of conservation of soil and the environment and the protection of water quality, and the possibility of applying the area to recreational purposes*'.

The *Primary Industries Corporation Act 1992* establishes the Primary Industries Corporation to administer the *Forestry Act 1959* and *Forestry Regulations*. The Primary Industries Corporation may recommend to the Governor-in-Council that the whole or part of a State Forest be declared a scientific area or feature protection area so as to preserve it as a sample of the natural environment of the State Forest concerned.

The *Marine Parks Act 1982* provides for the establishment of Marine Parks over tidal lands and tidal waters. A Marine Park includes the airspace above, the subsoil below and all marine products within a specified boundary. The Act requires the Government to consider public submissions in relation to the area of interest for a Marine Park and also provides for the preparation of zoning plans for each Marine Park.

Zoning provides for spatial separation of conflicting uses and results in a balanced approach to resource use and protection. A zoning plan which defines the various zones and their uses is developed in conjunction with extensive public consultation. The zoning plan is then released as subordinate legislation. Mining and exploration are possible in some areas of Queensland marine parks. Revocation of all or part of a marine park may only occur through a resolution of Parliament.

In the Great Barrier Reef Region, complementary Queensland marine parks are established to ensure adequate protection of the intertidal areas adjacent to, and Queensland waters which overlap with, the Great Barrier Reef Marine Park established under Commonwealth legislation.

Fish Habitat Areas (previously Fish Habitat and Wetland Reserves) are declared under the *Fisheries Act 1994* as part of the ongoing management of fisheries resources within Queensland. Fish Habitat Areas protect critical wetland habitats which sustain the fish and invertebrate stocks upon which recreational, commercial and indigenous fishing sectors depend. Declared Fish Habitat Areas are currently managed as 'A' or 'B' in recognition of their respective values to fisheries productivity and the level of disturbance acceptable in each.

The *Wet Tropics World Heritage Protection and Management Act 1993* provides complementary legislation to the Commonwealth legislation, the *Wet Tropics of Queensland World Heritage Area Conservation Act 1994*. The Wet Tropics Management Authority implements the management of the Wet Tropics area in order to ensure Australia's international obligations under the World Heritage Convention are met.

The *Coastal Protection and Management Act 1995* established the Coastal Protection Advisory Council, and provides for the protection, conservation, rehabilitation and management of the coast, its resources and biological diversity, with respect to the principles of the National Strategy for Ecologically Sustainable Development. It provides for the preparation of coastal management plans to address these issues.

In March 1995 the Queensland Government introduced Draft State Guidelines for tree clearing and a Preliminary Tree Clearing Policy was released on 18 December 1995, to apply to leasehold and other State lands. The guidelines provide controls over clearing on slopes, riparian strips, and endangered regional ecosystems (<10% of original vegetation remaining). On lands with regional ecosystems classed as 'of concern', i.e. where only 10% to 30% of original vegetation remains intact, clearing should be managed to ensure that at least 20% of the original vegetation remains. Further, no regional ecosystem is to be further cleared such that it moves from one class to another.

Local tree clearing guidelines are to be developed under the State Tree Clearing Policy, but are not yet completed. As of June 1997, 16 of 34 sets of guidelines had been approved regionally by the three Departments (Natural Resources, Primary Industries, and Environment & Heritage) with stakeholder inputs across Queensland. As of September 1998 34 sets of guidelines have been put in place to cover the leasehold and other Crown lands of queensland, and the development of guidelines for the remainder of the State are currently under consideration.

Vegetation management legislation is under review in Queensland for all lands (including freehold), and this includes a review of mechanisms to ensure protection of endangered ecosystems. Currently 105 (or 10%) of Queensland's regional ecosystems are classed as endangered (Sattler & Williams, in press).

Other measures for flora conservation in Queensland include: Vegetation Protection Orders administered by some local governments, the use of permits to clear the banks of watercourses under the *Water Resources Act 1989*, and the declaration of private properties as nature refuges managed by a conservation agreement under the *Nature Conservation Act 1992*. Currently there are 23 Nature Refuges and one Coordinated Conservation Area in place, covering an area of 11 173 hectares.

South Australia

The *National Parks and Wildlife Act 1972* provides for the establishment and management of reserves for public benefit and for the conservation of wildlife in a natural environment.

The reserves comprise national parks, conservation parks, game reserves, recreation parks and regional reserves. With the exception of recreation parks, reserves may only be abolished or their boundaries altered by a proclamation of the Governor, subject to a resolution passed by both Houses of Parliament.

Currently (as at 30 September 1998) South Australia has 18 National Parks covering an area of 4 337 431 ha, 216 Conservation Parks covering an area of 5 787 402 ha, five Wilderness Protection Areas covering an area of 70 074 ha, 45 Conservation Reserves covering an area of 273 965 ha, twelve Recreation Parks covering an area of 2994 ha, ten Game Reserves covering an area of 25 213 ha and seven Regional Reserves covering an area of 10 625 466 ha.

Management plans for each reserve are proposed and adopted by the Minister, after considering the comments and suggestions of the South Australian National Parks and Wildlife Council and representations from the public. Objectives prescribed in the Act for the management of reserves include: the preservation and management of wildlife, the preservation of features of geographical, natural or scenic interest, and the encouragement of public use and enjoyment of reserves. Management plans may also provide for the division of a reserve into zones which shall be kept and maintained under the conditions declared by the plan.

The South Australian National Parks and Wildlife Council, at the request of the Minister, can investigate and advise the Minister upon any matter referred to the Council for advice. The Council may also refer any matter affecting the administration of the Act to the Minister for consideration. Seven members are appointed to the committee by the Governor, and the Director is an *ex-officio* member.

The *Fisheries Act 1982* provides, *inter alia*, for the protection of aquatic habitat. Thirteen aquatic reserves have been proclaimed in South Australia pursuant to the Act. In addition, the *Fisheries Act (Aquatic Reserves) Regulations 1984* provides for limited access and/or limited fishing activities within the waters of most of the reserves. Other reserves are designated as non-entry, thereby affording complete protection to marine life within the reserve.

The *Forestry Act 1950* dedicates specific areas of Crown land as reserves to be managed exclusively for the purpose of forestry. Under the same Act, areas of indigenous forest habitat within forest reserves can be proclaimed and dedicated as Native Forest Reserves specifically for the conservation of flora and fauna. Native Forest Reserves are required to have a 'statement of purpose' for which they are established, and are protected under the Forestry Act from 'operations inconsistent with this purpose'. Proclamation occurs after approval from Parliament. Forest reserves are under the direct control of district managers and most occur in two major geographical regions of the State: South-East and Central. Flora and fauna on all forest reserves are protected under the *National Parks and Wildlife Act 1972*. Permits must be obtained from the Department of Environment, Heritage and Aboriginal Affairs and from the Department of Primary Industries and Resources before activities involving flora and fauna, other than observational activities, can be undertaken on forest reserves.

The *Historic Shipwrecks Act 1981* provides for the declaration of marine waters to protect historic shipwrecks. The legislation effectively gives protection to marine life in the designated area by prohibiting shipping, and by prohibiting diving or other underwater activities except in accordance with a permit issued by the Department of Environment, Heritage and Aboriginal Affairs.

In December 1991 the *Fisheries Act 1982* was amended to include provision for the establishment of Marine Parks. Under the Fisheries Act the Government may constitute as a Marine Park any waters, or land and waters, considered to be of national significance by reason of the aquatic flora or fauna of the aquatic habitat. Any changes to constituted marine parks can only be carried out by a resolution passed by both Houses of Parliament. One such Marine Park has since been proclaimed, the 44 000 ha Great Australian Bight Marine Park Whale Sanctuary, dedicated in 1995. A complementary 125 000 ha marine national park has been constituted in adjoining waters under the *National Parks and Wildlife Act 1972*.

The control and administration of all marine parks constituted under the Fisheries Act rests with the Minister of Primary Industries and Resources. The Minister must within two years of the constitution of the Marine Park propose a plan of management. Preparation of a plan includes public consultation and must consider the interest of Marine Parks which are contiguous with a reserve established under the *National Parks and Wildlife Act 1972*. Management arrangements must be coordinated with the management of any adjacent reserve established under the law of a State or the Commonwealth.

Once a Marine Park is constituted, provisions of the *Mining Act*, *Petroleum Act* and the *Petroleum (Submerged Lands) Act* do not apply unless proclaimed by the Governor.

The *Wilderness Protection Act 1992* provides for the protection of wilderness and the restoration of land to its condition before European colonisation. The Act established the five member Wilderness Advisory Committee, whose task is to assess all land in South Australia to identify areas that meet, or may be restored to, conditions matching the wilderness criteria, such as to warrant protection under the Act. The Act provides for the establishment of Wilderness Protection Areas and Zones, the latter reserve type applying where pre-existing mining is a temporary permitted activity.

A Wilderness Code of Management has been prepared to guide the management of Wilderness Reserves and public use of those areas. Five Wilderness Protected Areas have been proclaimed, all on Kangaroo Island. Management plans are a statutory requirement for Wilderness Reserves.

The *Crown Lands Act 1929* allows for the dedication of land for a range of purposes, including nature conservation and recreation. Under the Act, Conservation Reserves are proclaimed as an additional reserve type. There are currently forty-one Conservation Reserves vested under the care and control of the Minister, protecting areas of natural habitat throughout South Australia. This Act lacks the requirement for management plans and the degree of protection from other uses that apply to reserves under the other legislation.

Outside of protected areas the *Native Vegetation Act 1991* (which replaced the *Native Vegetation Management Act 1985)* requires landholders to obtain the consent of the Native

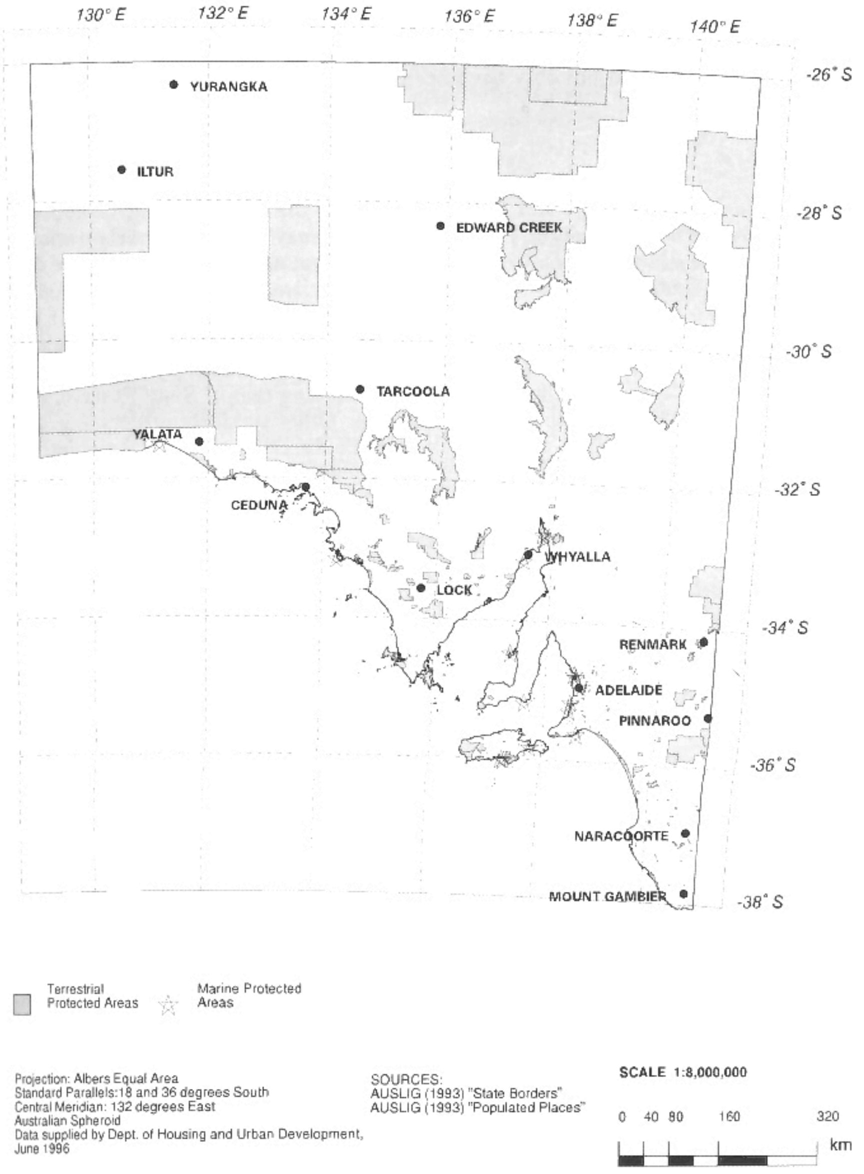


Figure 95. Terrestrial and marine protected areas of South Australia. Source: I.D.Cresswell and G.M.Thomas (1997), *Terrestrial and Marine Protected Areas in Australia*. Environment Australia Biodiversity Group, Canberra. Reproduced with permission.

Vegetation Authority before clearing can be undertaken. Approximately 900 Heritage Agreements have been created, covering around 600 000 hectares.

While not strictly designed for the conservation of flora *per se*, the *Pastoral Land Management and Conservation Act 1989* and the *Soil Conservation and Land Care Act 1989*, both have major implications for retaining native vegetation cover in this State. Sustainable use of the pastoral lands of South Australia, and the effective introduction of soil conservation and land care measures, provide greater protection of native flora over larger areas of the State than could possibly have been achieved through gazetted protected areas alone.

Tasmania

The *National Parks and Wildlife Act 1970* provides for the establishment of conservation areas by the Governor's proclamation. Conservation areas may include privately owned lands, subject to the consent of the owners. Conservation areas that are Crown land may be declared State Reserves or Game Reserves by Governor's proclamation. A proclamation which declares a State Reserve does not have effect until approved (or not disallowed) by both Houses of Parliament. State Reserves and Game Reserves may not be revoked unless the Governor's draft proclamation is first approved by each House of Parliament. This proclamation may give a name to the State Reserve including that of State Reserve, National Park, Nature Reserve, Historic Site or Aboriginal Site. Other statutory powers, e.g. granting of mining leases or forestry rights, do not apply in State Reserves or Game Reserves unless a management plan approved by both Houses of Parliament so provides.

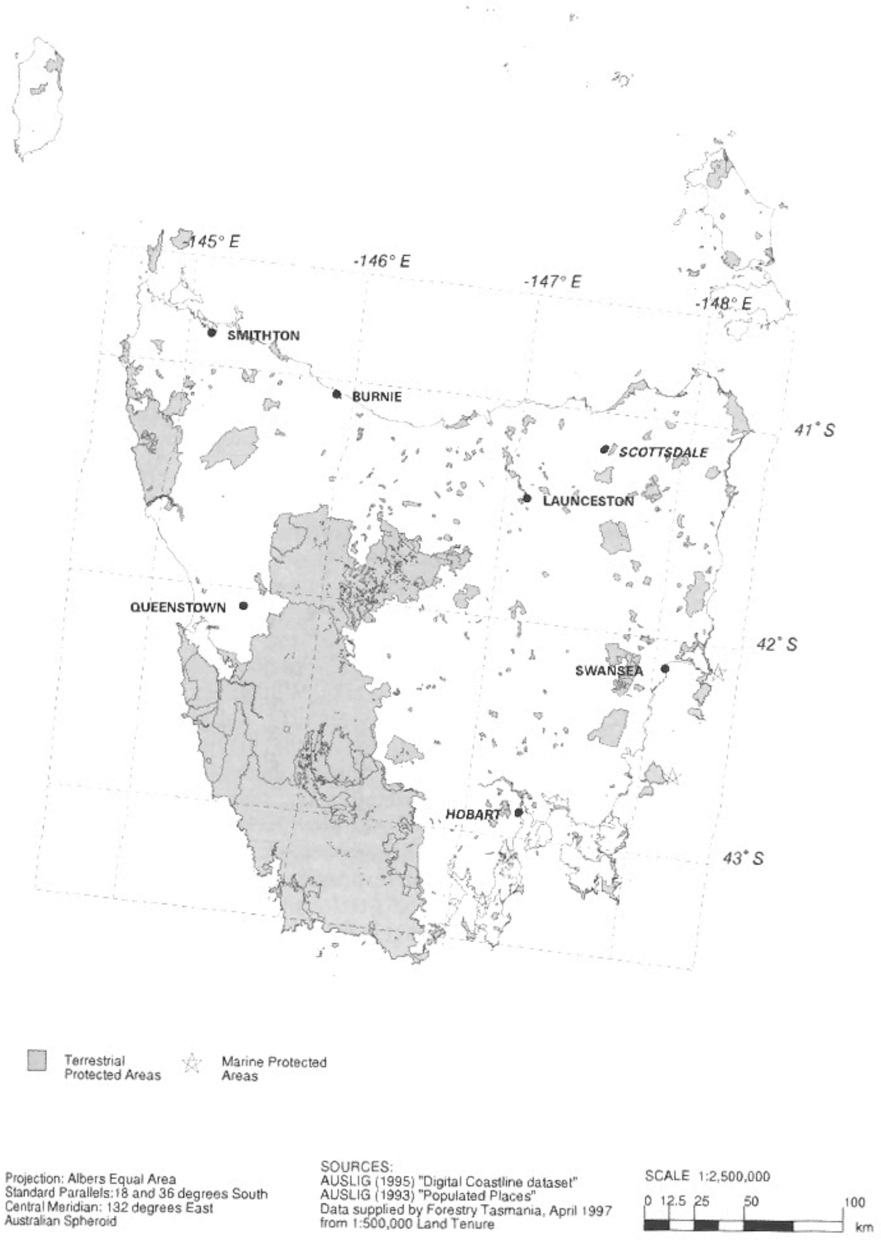
In Conservation Areas (some of which are named Wildlife Sanctuaries), wildlife and habitat are protected by regulations, but other activities such as mining and forestry are permitted. Management plans can provide additional protection. Section 22A–G of the *Forestry Act 1920* authorises preparation and approval of forest management plans in respect of Crown land that is both reserve land within the meaning of the *National Parks and Wildlife Act 1970*, i.e. set aside for a conservation purpose, and land in a state forest or timber reserve. Forestry operations may proceed in such areas with the concurrence of both the Parks and Wildlife Service, and Forestry Tasmania, subject to those operations not jeopardising the conservation values for which the area was declared.

National Parks are generally outstanding natural areas greater than 4000 hectares. Nature Reserves comprise areas of significant natural features reserved for nature conservation and scientific study. In Game reserves, management is aimed at nature conservation but permits may be given to enable the hunting of introduced or native game species in season.

Currently (as at 6 April 1998) Tasmania has 16 National Parks covering an area of 1 373 213 ha, 106 Conservation Areas covering an area of 403 906 ha, 54 Nature Reserves covering an area of 44 776 ha, 107 Forest Reserves covering an area of 49 720 ha, and 55 State Reserves covering an area of 18 142 ha.

Management plans are required to be prepared in respect of all areas proclaimed under the *National Parks and Wildlife Act 1970*. They must be publicly displayed, with comments being sought before finalisation and approval by the Governor. Where provision is made for use of a State Reserve other than as provided for in the Act, relevant parts of the management plan require the approval of both Houses of Parliament.

State Reserves, Game Reserves and Conservation Areas are administered by the Parks and Wildlife Service under the *National Parks and Wildlife Act 1970*, with advice from an Advisory Committee. Whereas some Conservation Areas are administered directly by the Service, there are, in addition, approximately 40 conservation areas where other government authorities or the owners are the managing authorities. The Service also manages Protected Areas, State Recreation Areas, Coastal Reserves etc., reserved under the *Crown Lands Act 1976*. Reserves administered include those covered by the sea and the sea itself. These areas are Marine Parks or Reserves. Administration is in cooperation with the Department of Primary Industry and Resources.



Projection: Albers Equal Area
Standard Parallels:18 and 36 degrees South
Central Meridian: 132 degrees East
Australian Spheroid

SOURCES:
AUSLIG (1995) "Digital Coastline dataset"
AUSLIG (1993) "Populated Places"
Data supplied by Forestry Tasmania, April 1997
from 1:500,000 Land Tenure

Figure 96. Terrestrial and marine protected areas of Tasmania. Source: I.D.Cresswell and G.M.Thomas (1997), *Terrestrial and Marine Protected Areas in Australia*. Environment Australia Biodiversity Group, Canberra. Reproduced with permission.

Under the Conservation Area Scheme under the *National Parks and Wildlife Act 1970,* private land may be proclaimed as a private reserve. Landholders enter an agreement, and the conditions are entered on the land title. Landholders may be provided with financial assistance for agreeing to protect wildlife or habitat.

Under the *National Parks and Wildlife Act 1970* and the *Land Titles Act 1980* private land conservation values may be protected by covenant on the title. Several covenants dealing with threatened species are currently being finalised.

Under the *Forestry Act 1920*, the Governor may, by proclamation in the *Government Gazette*, set aside land within a state forest as a forest reserve. Forest reserves are declared under section 20 of the *Forestry Act 1920* for the purposes of public recreation, preservation or protection of flora or fauna, or features of aesthetic, scientific or other value. Forest reserves may only be revoked with the approval of both Houses of Parliament.

The *Public Land (Administration and Forests) Act 1991* established the Public Land Use Commission, which advises on the allocation of public land, and therefore has a range of powers to protect native flora and fauna, including removing areas from logging zones.

The *Threatened Species Protection Act 1995* provides for the protection and management of native flora and fauna through listing of threatened species and a requirement for specific strategies to be implemented to provide action to promote the recovery of the listed species. The strategies also require the identification and management of threatening processes which impact on endangered species and identification of critical habitats.

Tasmania is also currently establishing a regionally based Land for Wildlife Scheme as part of its regional Bushcare extension arrangements under the Natural Heritage Trust.

Victoria

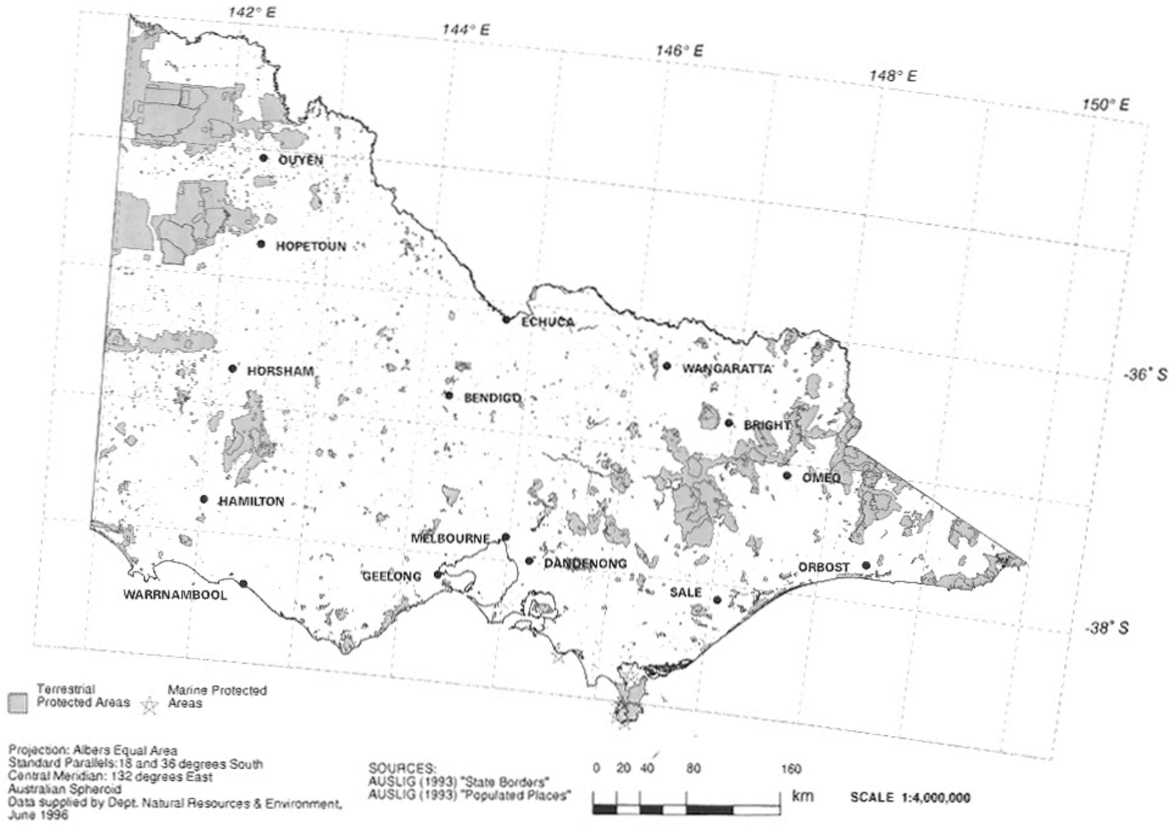
The *National Parks Act 1975* (together with the *National Parks (Alpine National Parks) Act 1989,* and the *National Parks (Wilderness) Act 1992*) provides for the establishment, protection and management of National Parks, State Parks, Wilderness Parks and other parks for the preservation and protection of the natural environment, indigenous flora and fauna, and features of scenic, archaeological, ecological, geological, historical or other scientific interest. The Act also provides for the protection and management of wilderness zones and remote and natural areas within National or State Parks, and designated water supply catchment areas in particular National Parks. The Act provides for the use of parks by the public for the purposes of enjoyment, recreation or education; for the encouragement and control of that use; and, in wilderness areas, for inspiration, solitude and appropriate self-reliant recreation. There are also provisions in the Act for the Director of National Parks to manage land not specifically reserved under the Act.

New parks or additions to existing parks are established by legislation which amends the appropriate schedules to the *National Parks Act 1975*. The Act requires the Director to prepare a management plan for each National, State, Wilderness and other Park. While the statutory Director of National Parks administers the *National Parks Act 1975*, Parks Victoria, a new organisation established as the service delivery agency for the Government's Parks program, is responsible for on-ground management of parks and reserves.

Currently (as at 30 June 1998) Victoria has 35 National Parks covering an area of 2 570 396 ha, six Marine and Coastal Parks covering an area of 46 660 ha, 416 Nature Conservation Reserves covering an area of 214 120 ha, three Wilderness Parks covering an area of 202 050 ha, 32 State Parks covering an area of 185 883 ha, and six 'other' parks covering an area of 35 638 ha.

The *Crown Land (Reserves) Act 1978* provides for the reservation of areas for a variety of purposes. Areas reserved under the Act include Nature Conservation Reserves (Flora and Fauna Reserves, Flora Reserves), Natural Features reserves and Marine Parks and Reserves.

The *Wildlife Act 1975* enables areas reserved under the *Crown Land (Reserves) Act 1978* for the propagation or management of wildlife, or for the preservation of wildlife habitat, or for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BENDIGO
BRIGHT
OMEO
HAMILTON
MELBOURNE
DANDENONG
GEELONG
ORBOST
SALE
WARRNAMBOOL
Terrestrial Protected Areas
Marine Protected Areas
Projection: Albers Equal Area
Standard Parallels:18 and 36 degrees South
Central Meridian: 132 degrees East
Australian Spheroid
Data supplied by Dept. Natural Resources & Environment, June 1996
SOURCES:
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AUSLIG (1993) "Populated Places"
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Figure 97. Terrestrial and marine protected areas of Victoria.
Source: I.D.Cresswell and G.M.Thomas (1997). *Terrestrial and Marine Protected Areas in Australia*. Environment Australia Biodiversity Group. Canberra. Reproduced with permission.

any other purpose, to be classified as State Wildlife Reserves or Nature Reserves. The Secretary to the Department of Natural Resources and Environment is required to prepare as soon as practicable a plan of management for each State Wildlife Reserve and Nature Reserve. The Minister may adopt or vary such plans.

The *Reference Areas Act 1978* provides for Reference Areas to be proclaimed by the Governor-in-Council, and for the Minister to issue directives for their protection, control and management. Reference Areas are areas of ecological interest and significance, and are managed under the Act to ensure their long term viability to conserve these ecological attributes.

The *Flora and Fauna Guarantee Act 1988* protects Victoria's flora and fauna for 'varied and future needs', through the establishment and management of State reserves, refuges and conservation areas.

The *Heritage Rivers Act 1992* provides for the protection of heritage rivers and natural catchment areas and requires a management plan to be prepared for each river and catchment area.

The *Catchment and Land Protection Act 1994* establishes a peak Catchment Management Council, nine Catchment Management Authorities and one Catchment and Land Protection Board across the State to oversee the sustainable management of catchments, which includes the conservation of flora as an integral land management activity. The Act requires the preparation of Regional Catchment Strategies and is aimed at setting up a framework for the integrated management and protection of catchments. It outlines the general duties of landowners in addition to containing provisions for the control of pest plants and animals.

The *Coastal Management Act 1995* established the Victorian Coastal and Bay Management Council, to oversee the long term planning of the coast to ensure the protection of significant environmental features, and the sustainable use of natural coastal resources. It also provides for the establishment of regional Coastal Boards, and the development of a Victorian Coastal Strategy which requires the development of Coastal Action Plans, including detailed environmental planning.

The *Victorian Conservation Trust Act 1972* established the Victorian Conservation Trust (now known as the Trust for Nature Victoria) as an independent body to conserve areas of ecological significance through the acceptance of community conservation funds such as gifts and bequests. By 1996, in conjunction with the State Government, the Trust for Nature Victoria had negotiated voluntary covenants over more than 180 properties covering more than 6500 ha, and was negotiating a further 130 properties covering over 5000 ha (ANZECC Working Group on Nature Conservation on Private Land, 1996). Outright purchase of these properties would have cost an estimated $20 million. The Trust for Nature Victoria has also initiated a revolving fund with a small capital base to buy, covenant and resell land, in order to provide maximum flexibility in achieving its conservation goals.

Clearing of native vegetation in Victoria was severely restricted by the amendment in 1989 of the *Planning and Environment Act 1987,* which in practice stops broadscale clearing on blocks greater than 0.4 ha.

The voluntary 'Land for Wildlife Scheme', begun in 1981 and administered by the Department of Natural Resources and Environment and the Bird Observers Club of Australia, encourages landholders to conserve native habitat. However agreements under this scheme may be revoked at any time and cover the current landholder only.

Voluntary Land Management Cooperative Agreements are a component of the Flora and Fauna Guarantee Program under the *Conservation, Forests and Lands Act 1987* and may cover public, Crown lease or freehold land. They are designed to encourage cooperative management and conservation of flora and fauna. Long-term covenants may be linked to the title. Also of relevance to flora conservation under the *Conservation, Forests and Lands Act 1987* is the establishment of codes of practice for land management covering various aspects of land degradation. Codes of practice are not legally binding.

In December 1997 Victoria launched its Biodiversity Strategy, which contains the major strategic direction for flora and fauna conservation within a regional context. The strategy is in three parts and sets out broad principles and challenges for sustaining the 'living wealth' of the State together with directions in management.

Western Australia

The protection of flora throughout Western Australia is a function of the Department of Conservation and Land Management (CALM) as is management of Western Australia's conservation reserve system under the *Conservation and Land Management Act 1984*.

Statewide protection of all taxa is effected under the Wildlife Conservation Act 1950. On Crown land protected flora cannot be taken without a licence and protected flora taken on private land cannot be sold without a licence having been issued. A number of species, in addition to declared rare flora, have been prohibited from being taken on Crown land because of the impact of commercial harvesting on them. Access to Crown land for the purpose of commercially harvesting flora is also subject to the consent of the relevant management body of the land. Access to conservation reserves for this purpose is not permitted. A management program for the commercial harvesting of protected flora is in place.

Protected flora that is threatened may be declared 'rare flora' by the Minister under the *Wildlife Conservation Act 1950* to provide it with a special level of protection (the Minister's written consent is required to take declared rare flora irrespective of the land tenure where it occurs). Regional or district management programs for declared rare flora and recovery plans for individual taxa are produced and implemented.

Land can be reserved for conservation purposes by the Minister under the *Land Administration Act 1997* (which replaced the *Land Act 1933*). If a reserve is made Class A under this Act, e.g. a reserve providing for the conservation of flora, and it is subsequently proposed to amend its purpose or significantly change the reserve, then the proposal has to be tabled in Parliament by the Minister, where it may be disallowed.

Under the *Conservation and Land Management Act 1984* national parks, conservation parks and nature reserves (for the conservation of flora and fauna) are automatically vested in the National Parks and Nature Conservation Authority. Management plans for these reserves have to achieve or promote the reserve's purpose. Other reserves for conservation and recreation subject to the *Conservation and Land Management Act 1984* are designated section 5(g) or 5(h) reserves.

As at 30 June 1998 Western Australia has 4 874 282 ha of National Park, 117 324 ha of Conservation Park, 10 772 271 ha of Nature Reserve, and 147 785 ha of Section 5(g) reserves vested in the National Parks and Nature Conservation Authority.

The National Parks and Nature Conservation Authority is established under the *Conservation and Land Management Act 1984* to develop policies for preserving the natural environment, to submit proposed management plans for the reserves vested in it to the Minister for approval, to monitor the carrying out of approved management plans and to encourage public appreciation of nature. On the Authority's recommendation, the Minister may classify reserves or parts of reserves vested in the Authority for such purposes as prohibited or restricted access or, in the case of a national park, for the purpose of a wilderness area. Classified areas are in effect management zones.

Under the *Conservation and Land Management Act 1984*, the Governor may reserve Western Australian waters (marine and estuarine habitats) as a marine nature reserve, a marine park, or a marine management area. Marine flora cannot be taken in marine reserves without lawful authority. Marine Parks comprise 1 013 940 ha and marine nature reserves 132 000 ha. All of these reserves are vested in the Marine Parks and Reserves Authority which has functions analogous to those of the National Parks and Nature Conservation Authority.

Under the *Fish Resources Management Act 1994*, the Minister for Fisheries may set aside fish habitat protection areas in any Western Australian waters which are not in a marine reserve established under the *Conservation and Land Management Act 1984*.

State forests and timber reserves are reserved by the Governor and vested in the Lands and Forest Commission under the *Conservation and Land Management Act 1984*. These reserves are managed for multiple purposes including conservation, recreation, timber production on a sustained yield basis and water catchment protection. As the vested body for State forests and timber reserves, the Lands and Forest Commission develops policies to promote the purposes of these reserves, submits proposed reserve management plans to the Minister for approval and monitors the implementation of approved management plans. The area of State forest and timber reserves as at 30 June 1998 was 1 727 514 ha and 141 550 ha respectively. There are 82 723 ha of 5(g) reserves vested in the Lands and Forest Commission. Forest produce cannot be removed from State forests, timber reserves and Crown land without authorisation under the *Conservation and Land Management Act 1984*. Forest produce includes sandalwood, and the sustainable removal of sandalwood from Crown land and alienated land is subject to this Act and the *Sandalwood Act 1929*.

Under the *Soil and Land Conservation Act 1945* landholders wishing to clear more than one hectare of native vegetation are required to obtain permission from Agriculture Western Australia (Commissioner of Soil and Land Conservation). Clearing can be prevented where it is likely to result in a land degradation hazard, or where rare flora is involved. Areas not allowed to be cleared must be fenced to prevent grazing.

In May 1995 the Western Australian Government introduced additional clearing controls under the *Soil and Land Conservation Act 1945*, designed to prevent clearing in shires or on individual farms which have been extensively cleared.

Specific measures include:

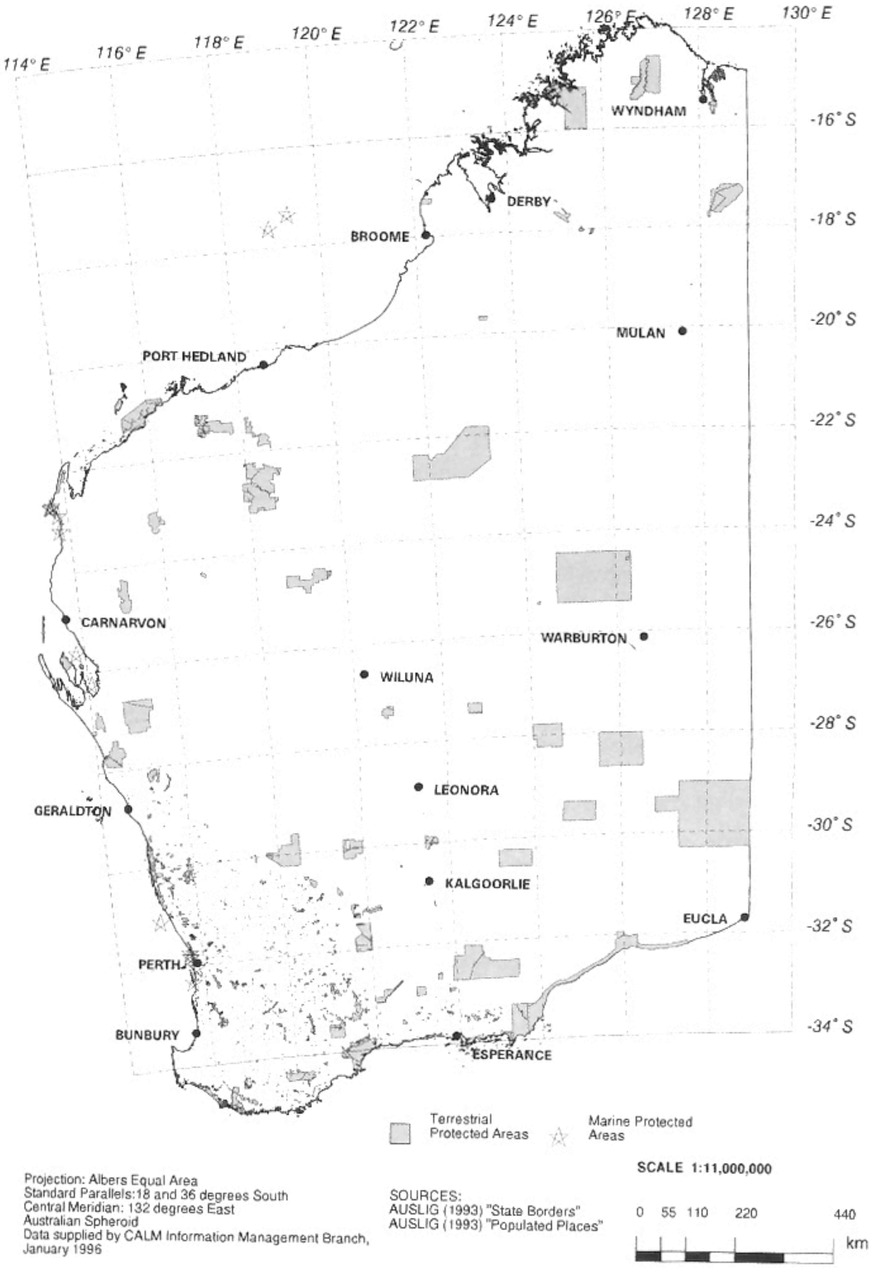
- land clearing being restricted if less than 20% of the individual property is covered with remnant vegetation or deep rooted perennial vegetation;
- land clearing being discouraged in country shires with less than 20% of remnants (including nature reserves) but being allowed where landholders can clearly prove that further clearing will not cause land degradation or threaten native species;
- if the property has more than 20% but the shire has less than 20% of remnants, the proponent being required to demonstrate the clearing will not threaten important conservation values or cause land degradation.

Land clearing proposals that may have a significant effect on the environment are referable to the Environmental Protection Authority for its consideration for environmental impact assessment under the *Environmental Protection Act 1986*. Under this Act, enforceable environmental protection policies which regulate land clearing, related threats to native vegetation and the environment generally can be made (e.g. the *Environmental Protection (South West Agricultural Zone Wetlands) Policy 1997*).

Under the *Conservation and Land Management Act 1984*, provision is also made for landowners to enter agreements to manage private land as if it were a nature reserve or one of the other categories of conservation reserve that the Act applies to. The details of the agreements would be worked out between the landholder and CALM, although no agreements had been put in place as at June 1998.

CALM also operates a 'Land for Wildlife' scheme which provides assistance to landholders registered under the scheme to protect nature (biodiversity) conservation values on their land. CALM also provides advisory assistance to landholders and encourages the retention and management of private native vegetation, and is developing a voluntary nature conservation covenanting scheme.

Agriculture Western Australia, in conjunction with CALM, administers the Remnant Vegetation Protection Scheme started in 1988, under the *Soil and Land Conservation Act 1945*. The Scheme provides financial assistance for fencing remnant vegetation. Applications are assessed on the conservation value of the vegetation, and the successful applicants are required to enter into a 30 year covenant that precludes the use of the land for any purpose that would be detrimental to the vegetation. In the ten years the scheme has been operating, 975 areas of remnant vegetation, totalling over 43 000 hectares, have been protected.



Projection: Albers Equal Area
Standard Parallels:18 and 36 degrees South
Central Meridian: 132 degrees East
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Data supplied by CALM Information Management Branch, January 1996

SOURCES:
AUSLIG (1993) "State Borders"
AUSLIG (1993) "Populated Places"

Figure 98. Terrestrial and marine protected areas of Western Australia. Source: I.D.Cresswell and G.M.Thomas (1997), *Terrestrial and Marine Protected Areas in Australia*. Environment Australia Biodiversity Group, Canberra. Reproduced with permission.

Under the *Country Areas Water Supply Act 1947*, controls exist over clearing of native vegetation in six catchments in the south-west of Western Australia. Applications to clear are made to the Water and Rivers Commission, and if an application is refused, the landowner may claim compensation.

There are still about 800 properties in Western Australia under the Conditional Purchase Lease System, which requires the blocks to be half-cleared before they can be converted to freehold. The Department of Land Administration has not enforced this requirement at the operational level for several years, although technically it still stands.

Past clearing practices in the agricultural region have resulted in extensive land salinisation. The Western Australian Government's 'Salinity Action Plan' of 1996 has set a number of objectives to manage salinity including protection and maintenance of biological and physical diversity within agricultural areas, and substantial revegetation with woody perennials.

A Memorandum of Understanding for the Protection of Remnant Vegetation on Private Land in the Agricultural Region of Western Australia was signed in 1997 by the following agencies to coordinate action throughout the State: CALM; the Department of Environmental Protection; Agriculture Western Australia; the Water and Rivers Commission; the Environmental Protection Authority and the Commissioner for Soil and Land Conservation.

On Crown land leased for pastoral purposes, the Pastoral Lands Board established under the *Land Administration Act 1997* has a responsibility to ensure that pastoral leases are managed on an ecologically sustainable basis. A pastoral lessee cannot clear land, sow non-indigenous pastures or carry out non-pastoral activities on a pastoral lease without a permit from the Pastoral Lands Board. The Board cannot issue such permits unless environmental conservation requirements have been complied with under the *Agriculture and Related Resources Protection Act 1976*, the *Environmental Protection Act 1986*, the *Soil and Land Conservation Act 1945*, the *Wildlife Conservation Act 1950* or any other applicable law which relates to environmental conservation on a pastoral lease.

In recognition of the vulnerability of rail and roadside vegetation to disturbance and degradation and its importance to regional flora conservation, the 'Roadside Conservation Committee' has been established which co-ordinates and promotes the conservation and effective management of rail and roadside vegetation for the benefit of the environment and the people of Western Australia.

To better facilitate the protection of remnant vegetation communities in the Perth Metropolitan Region, in the context of the Western Australian Government's 'Urban Bushland Strategy', a proposed 'Perth's Bushplan' is being developed.

Collecting Permits, Import and Export Permits

Each Australian State and Territory has a system of permits governing the collection of native plants and animals for all purposes, including scientific studies. These regulations, managed by various organisations, are backed in many cases by heavy penalties. The import and export of plants is controlled by the *Wildlife Protection (Regulation of Exports and Imports) Act (1982)*, and has particular impact on material which is designated as Type material (at export or subsequently), or species listed on the schedules of the *Convention on International Trade in Endangered Species*. Information on permit requirements is available from the ABRS Website.

Acknowledgments

I would like to give thanks for the valuable help given to me on previous drafts of this chapter by Doug Brown, Gwen Shaughnessy and Peter Bridgewater. I would also like to thank Peter Bosworth, Peter Copley, Rob Dick, Caroline Douglass, Tim Ellis, Simon Hancocks, Clare Hasewski, Bill Logan, John Lumb, Bruce Male, John Neldner, Tony Orchard, Sandra Potter and Paul Sattler for providing input, advice and comments to clarify the text.

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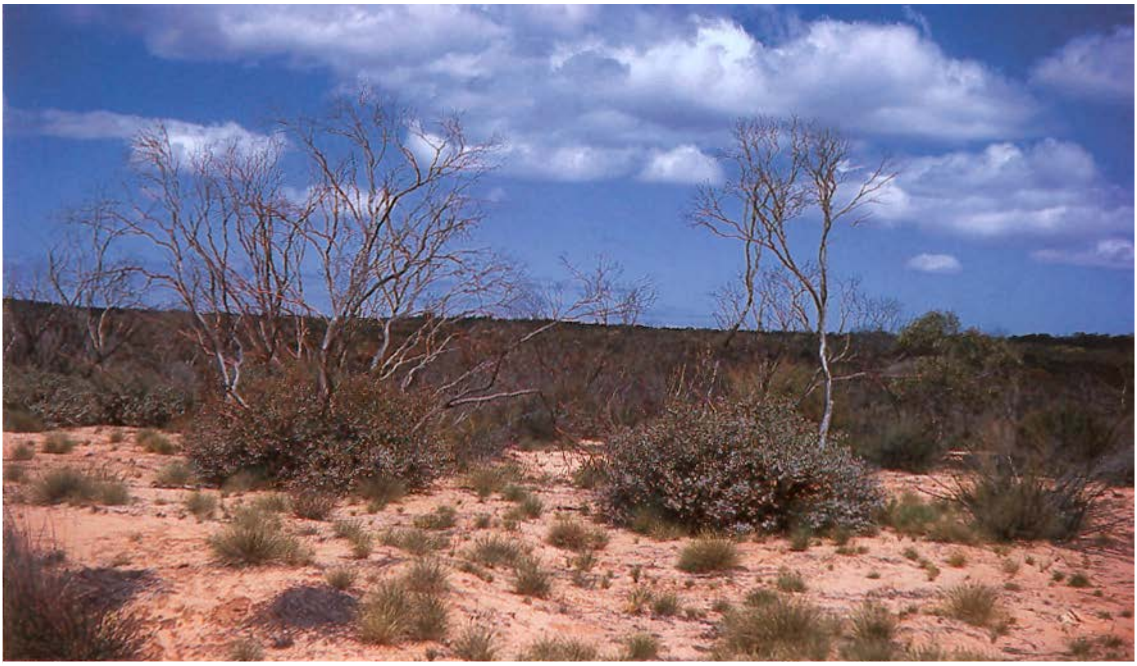

Figure 99. Mallee eucalypts regenerating (sprouting from lignotuber) after fire, Iron Duke, S.A. Photograph — A.E.Orchard.

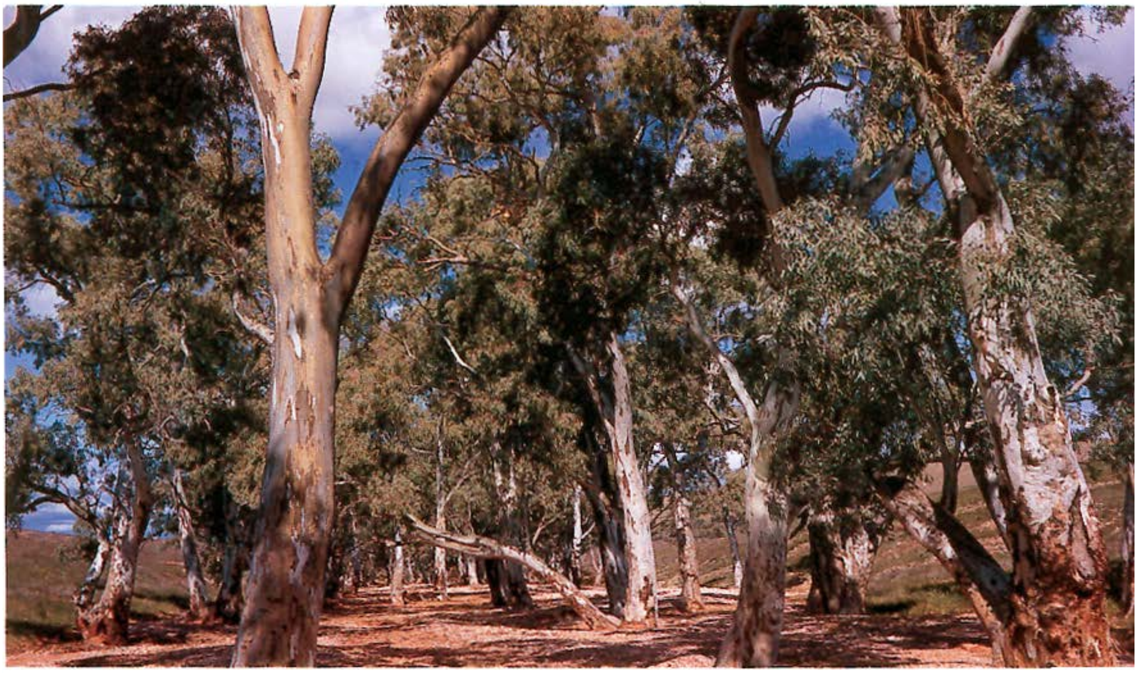

Figure 100. Riverine woodland of *Eucalyptus camaldulensis*, Kanyaka Creek, Flinders Range, S.A. Photograph — G.F.Halliday.

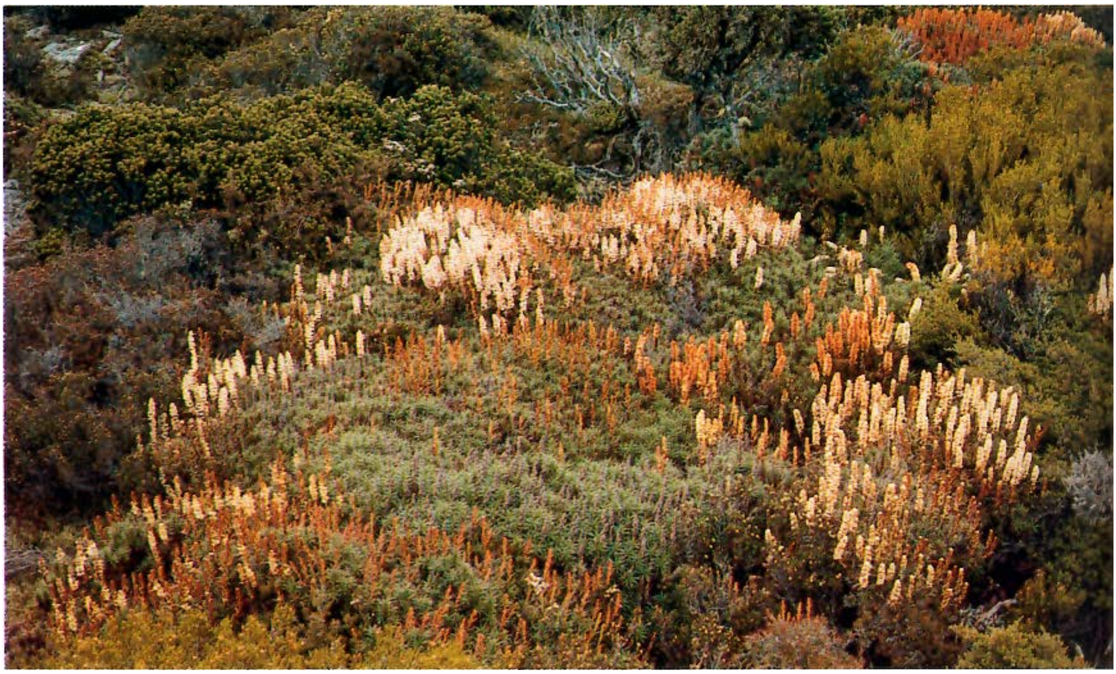

Figure 101. Alpine heathland, dominated by *Richea scoparia* and *Orites acicularis*, Projection Bluff, Tas. Photograph — S.J.Jarman.

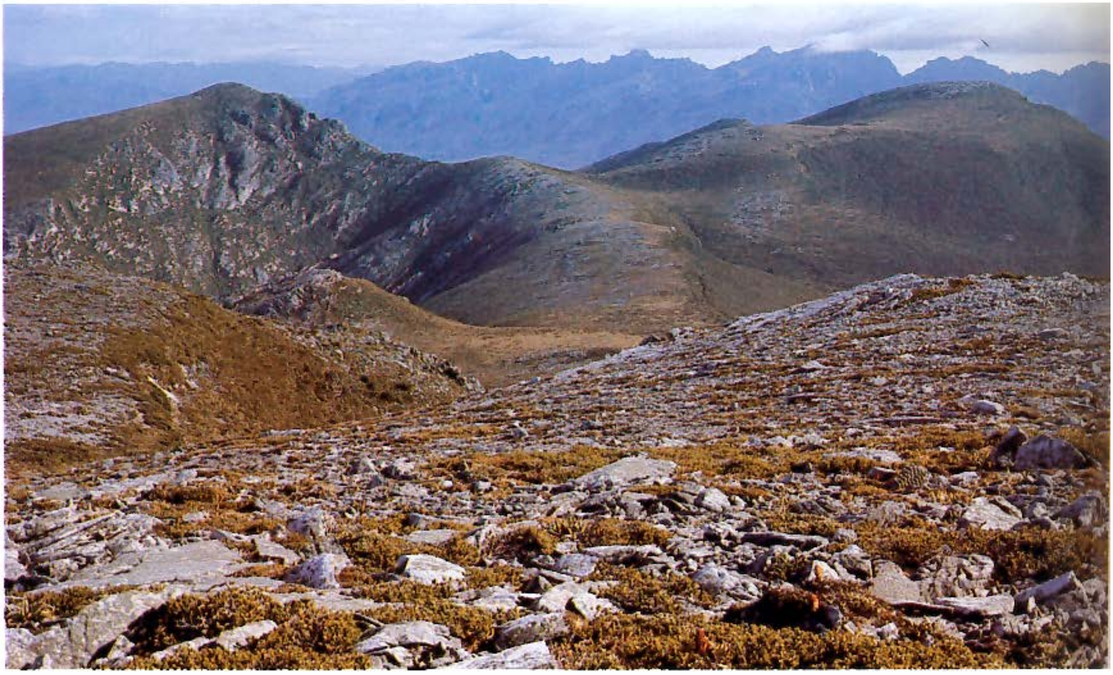

Figure 102. Alpine heathland of *Eucalyptus vernicosa*/*Richea scoparia* and feldmark mosaic on Precambrian metamorphic rock types, Mt Norold, Tas.
Photograph — S.J.Jarman.

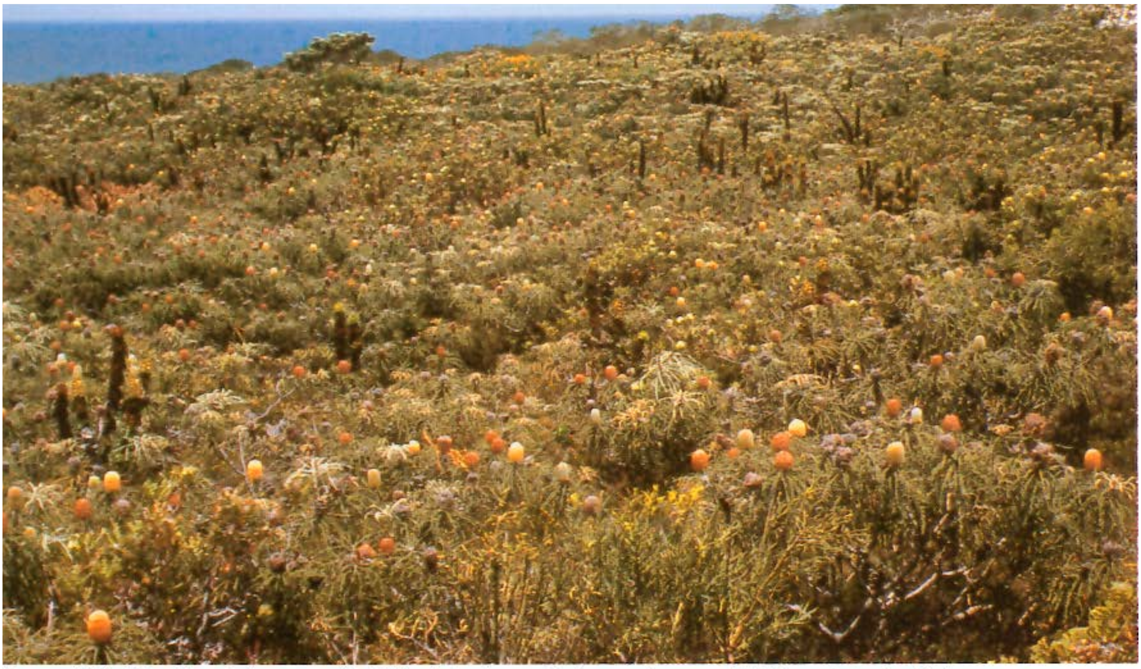

Figure 103. Shrubland (kwongan) of *Banksia baxteri*, *B. speciosa* and *Hakea victoria*, East Mount Barren, W.A. Photograph — K.Thiele (ANBG).

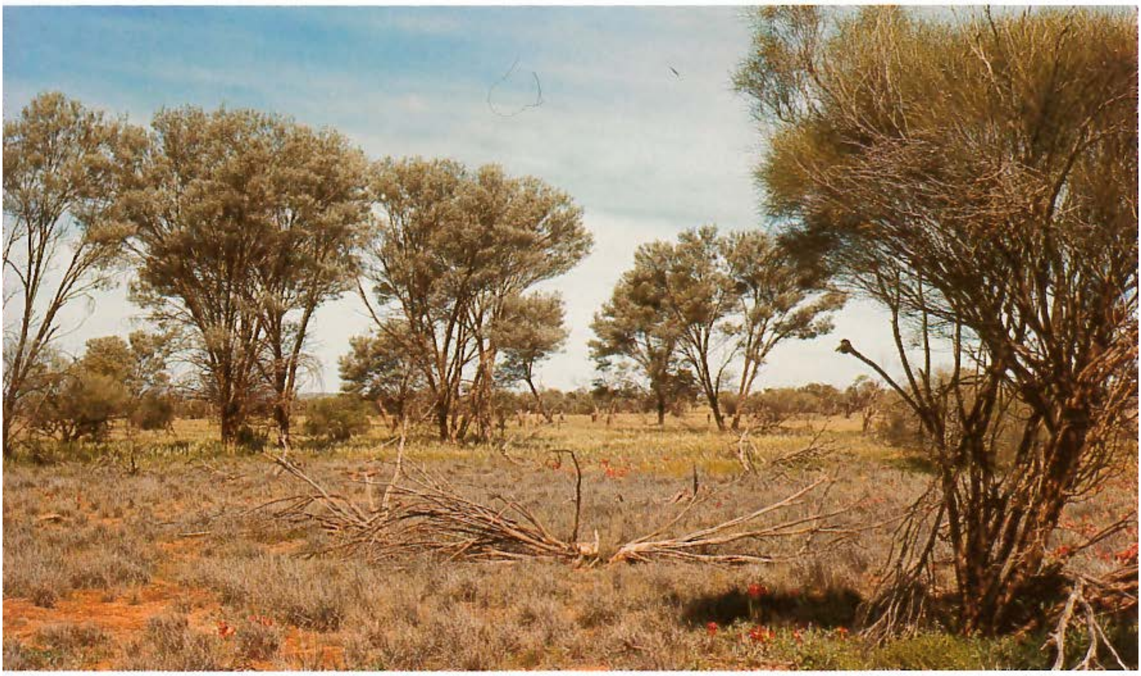

Figure 104. Open grassy woodland of Mulga (*Acacia aneura*) and *A. burkittii*, Koonamore Vegetation Reserve, S.A.
Photograph — M.D.Crisp.

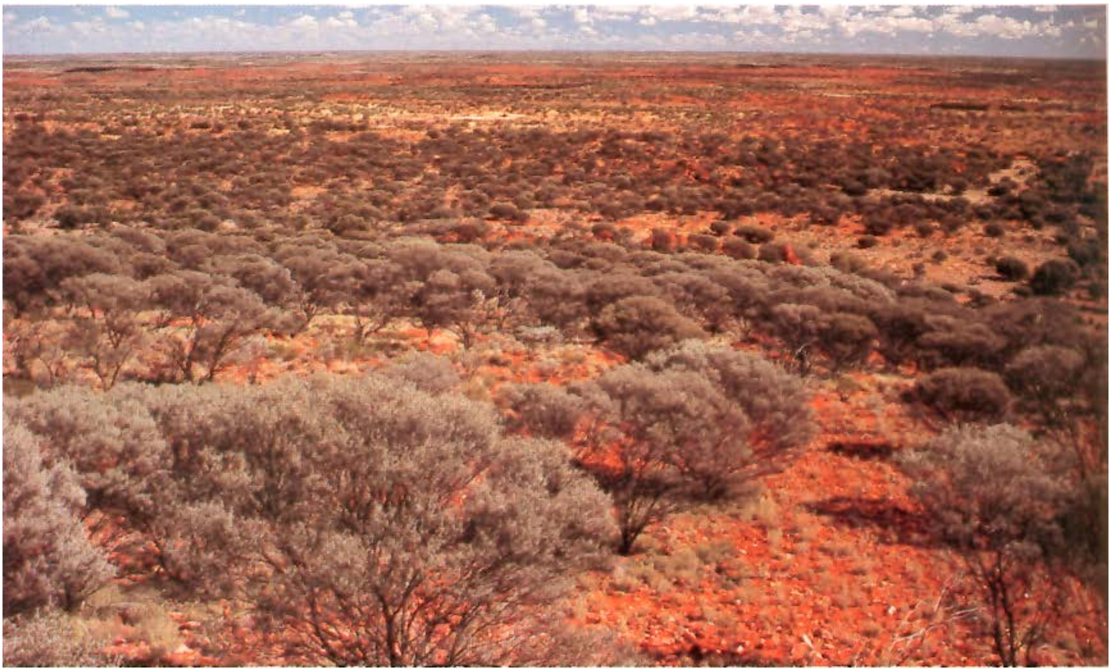

Figure 105. *Acacia aneura* grassy shrubland near Mt Connor, N.T.
Photograph — K.Thiele (ANBG).

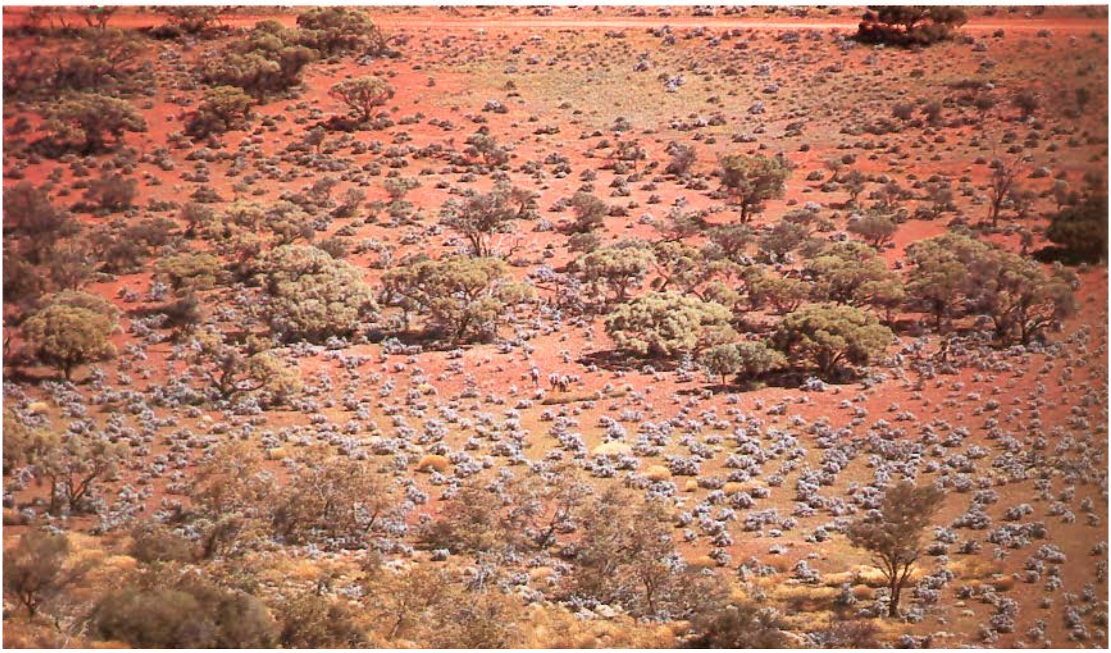

Figure 106. Bluebush (*Maireana sedifolia*) shrubland with occasional mallee *Eucalyptus* and *Acacia* spp., near Mt Partridge, Gawler Range, S.A.
Photograph — A.E.Orchard.

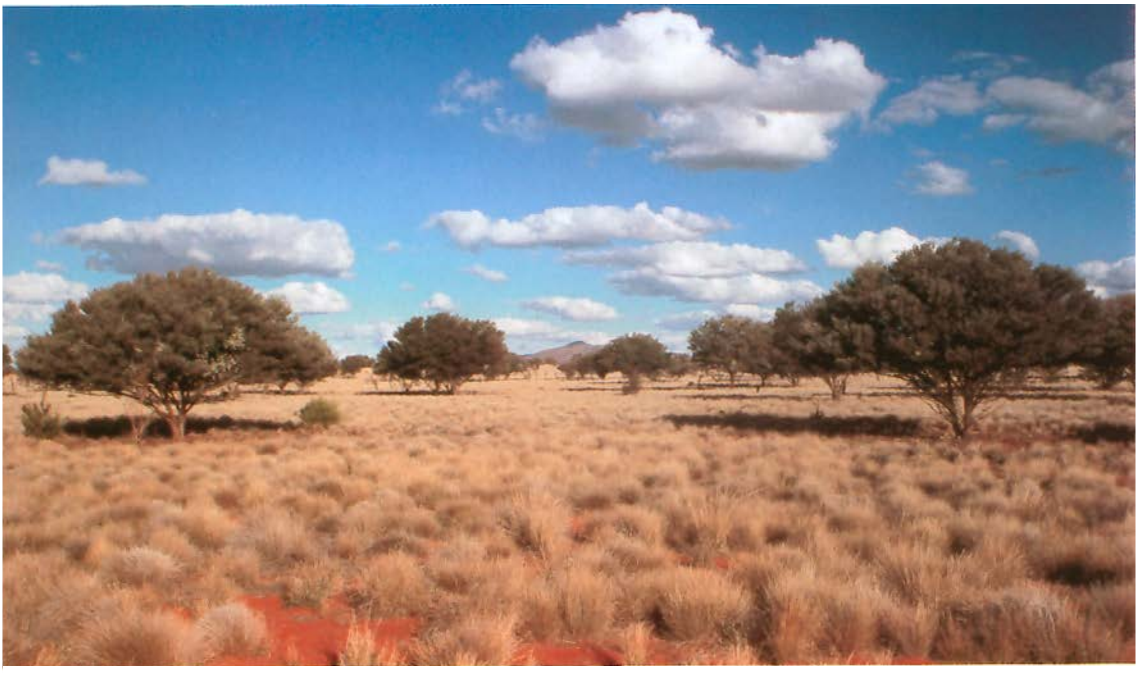

Figure 107. *Aristida* tussock grassland with scattered Mulga (*Acacia aneura*), Mulga Park HS, N.T. Photograph — K.Thiele (ANBG).

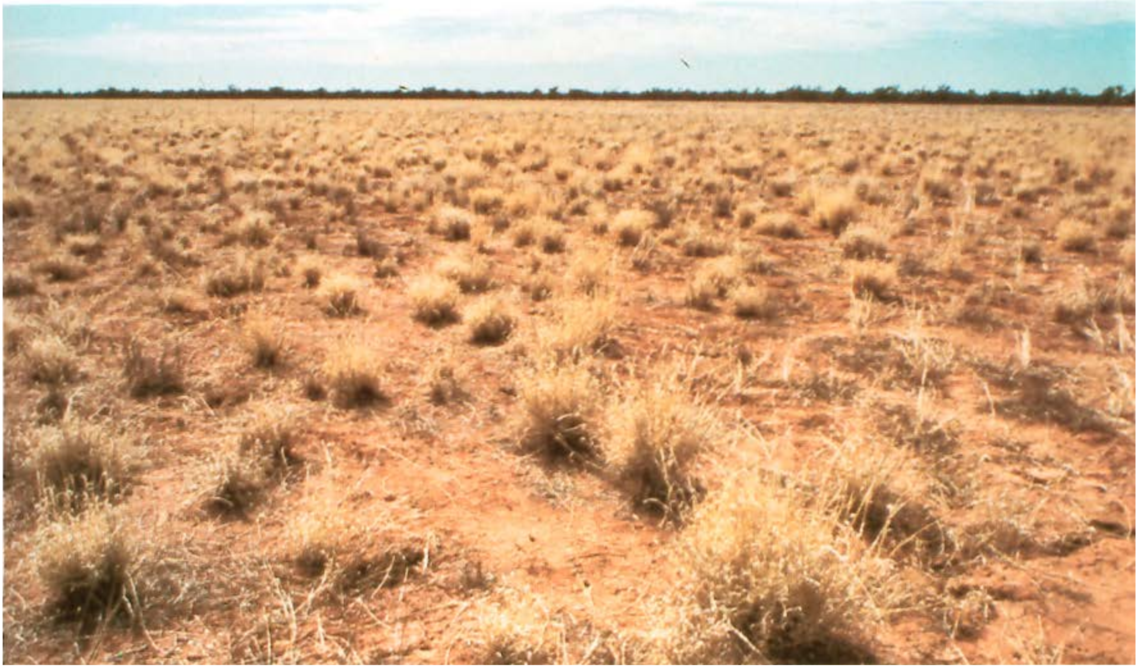

Figure 108. Mitchell grass (*Astrebla* spp.) grassland, 70 km N of Cunnumulla, Qld. Photograph — M.J.Fagg (ANBG).

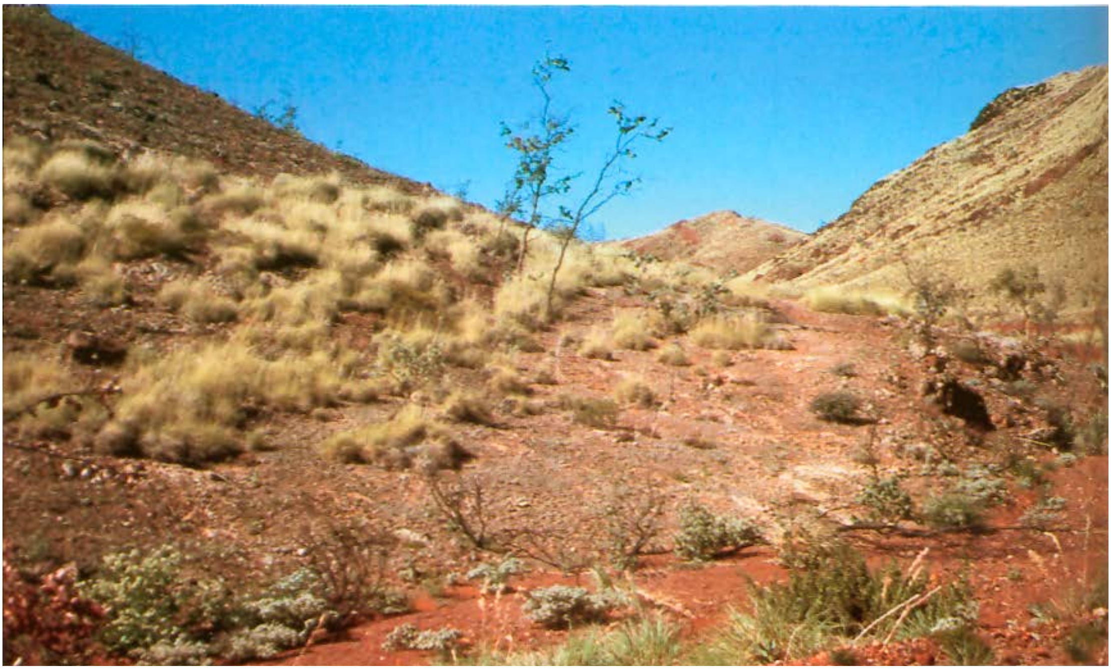

Figure 109. *Triodia* sp. hummock grasses on Ironstone Hills near Marble Bar, W.A.
Photograph — G.Butler (ANBG).

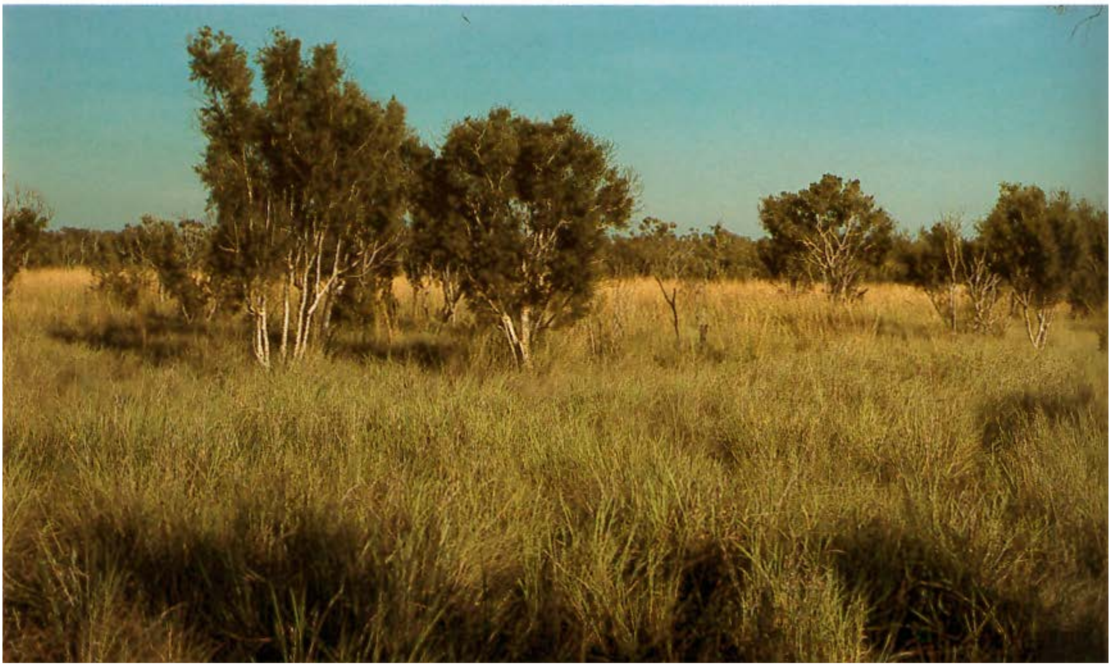

Figure 110. Seasonally inundated grassland (*Dicanthium* sp.) with scattered *Melaleuca* sp., Gregory National Park, N.T.
Photograph — D.B.Foreman.

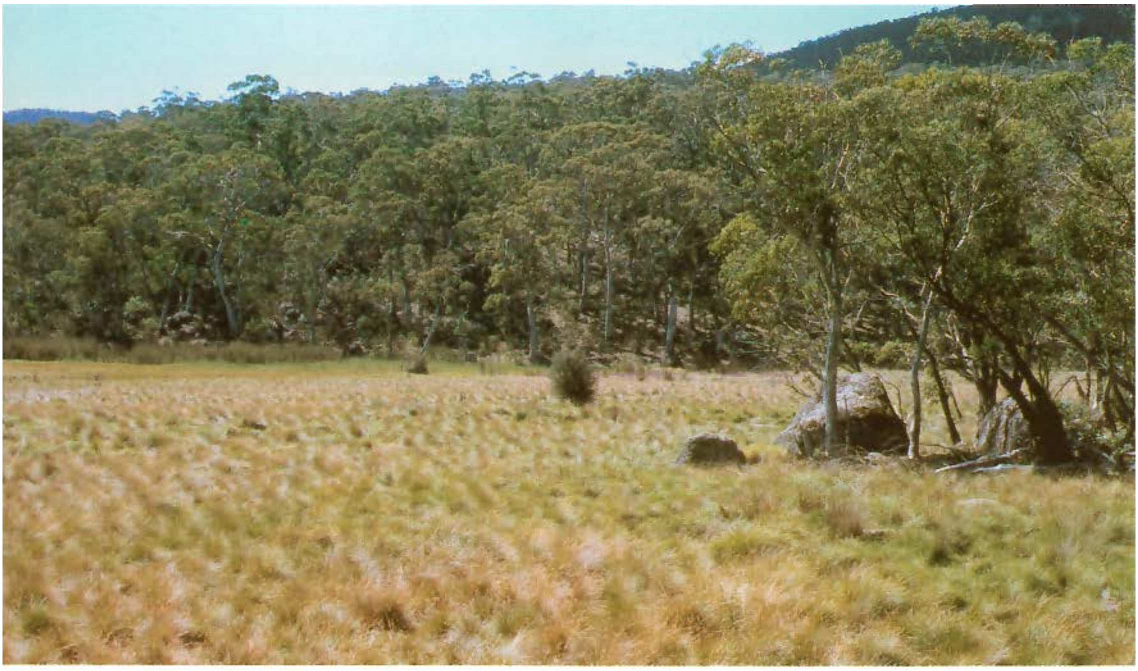

Figure 111. Alpine tussock grassland, Namadji National Park near Tharwa, A.C.T.
Photograph — M.J.Fagg (ANBG).

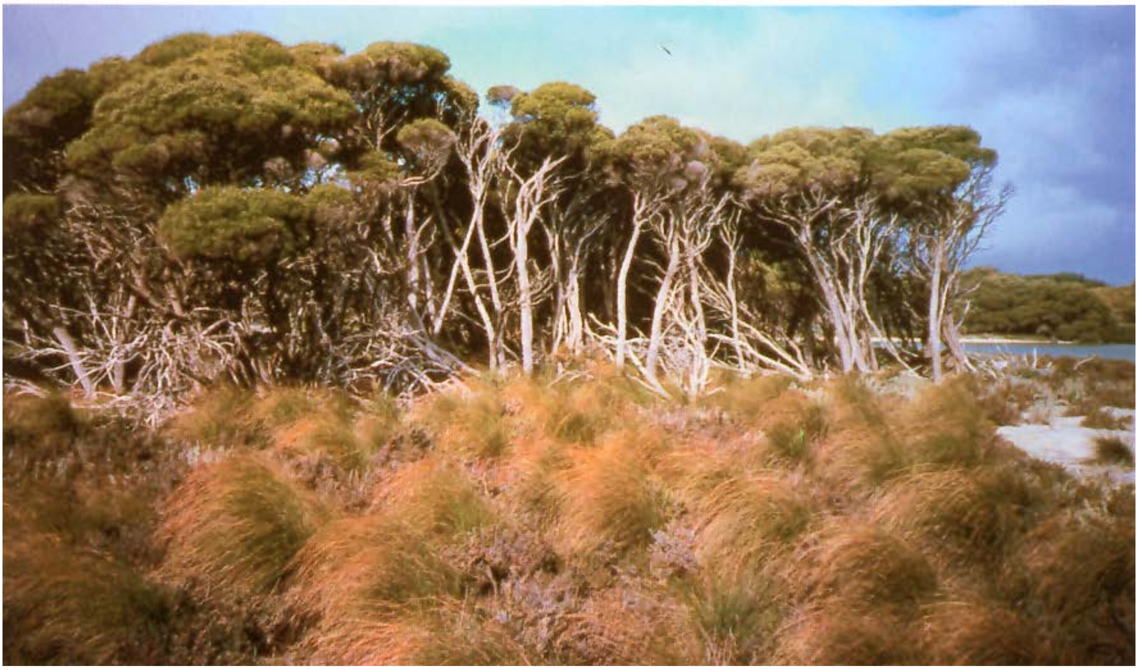

Figure 112. *Stipa variabilis* grassland, with *Rhagodia* sp., *Atriplex* sp. and *Melaleuca lanceolata*, near Lake Sirius, Rottnest Island, W.A.
Photograph — R.Purdie (ANBG).

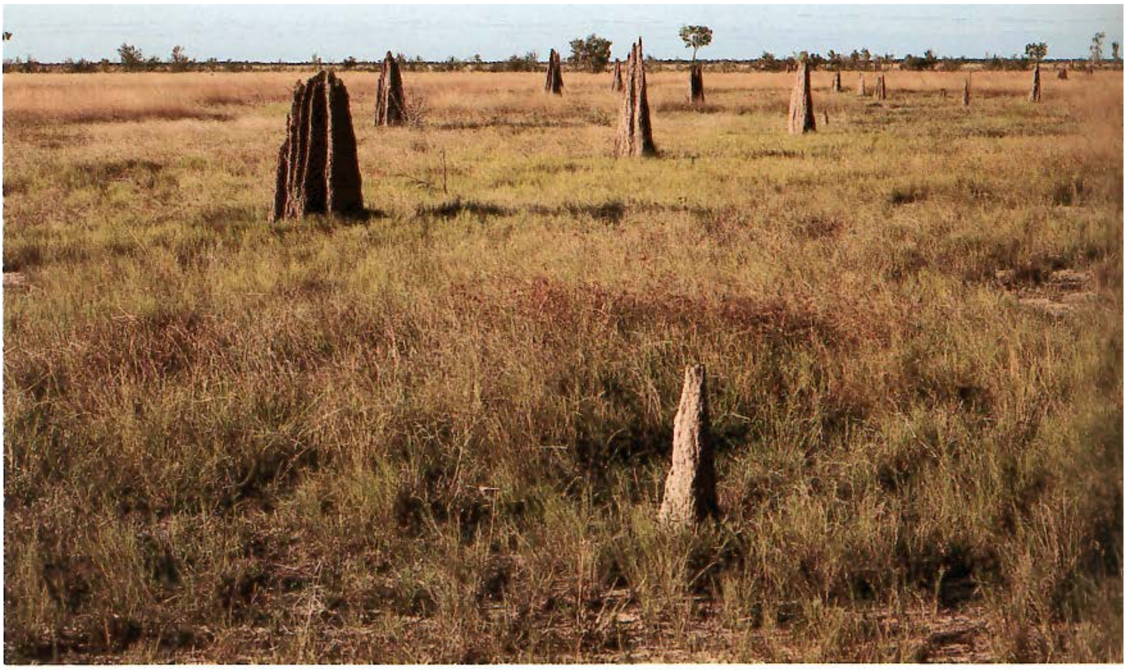

Figure 113. *Sporobolus virginicus* dominated grassland, near Kowanyama, Qld.
Photograph — V.J.Nelder.

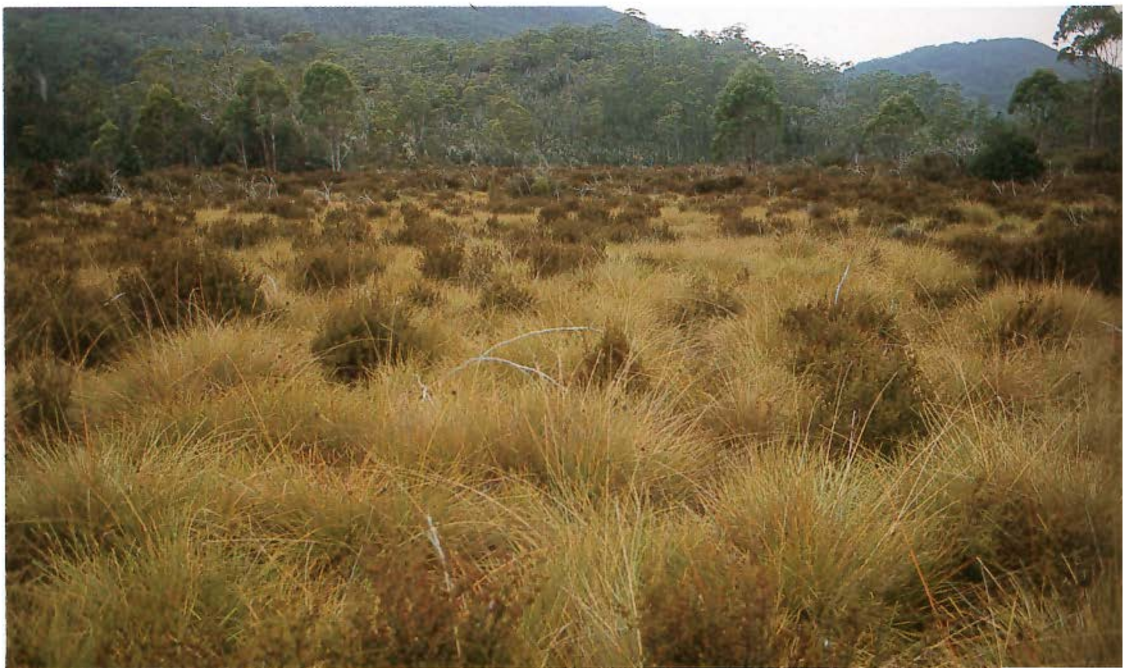

Figure 114. Buttongrass moorland (*Gymnoschoenus sphaerocephalus*) with *Baeckea gunniana*, Jane River Track, Tas.
Photograph — S.J.Jarman.

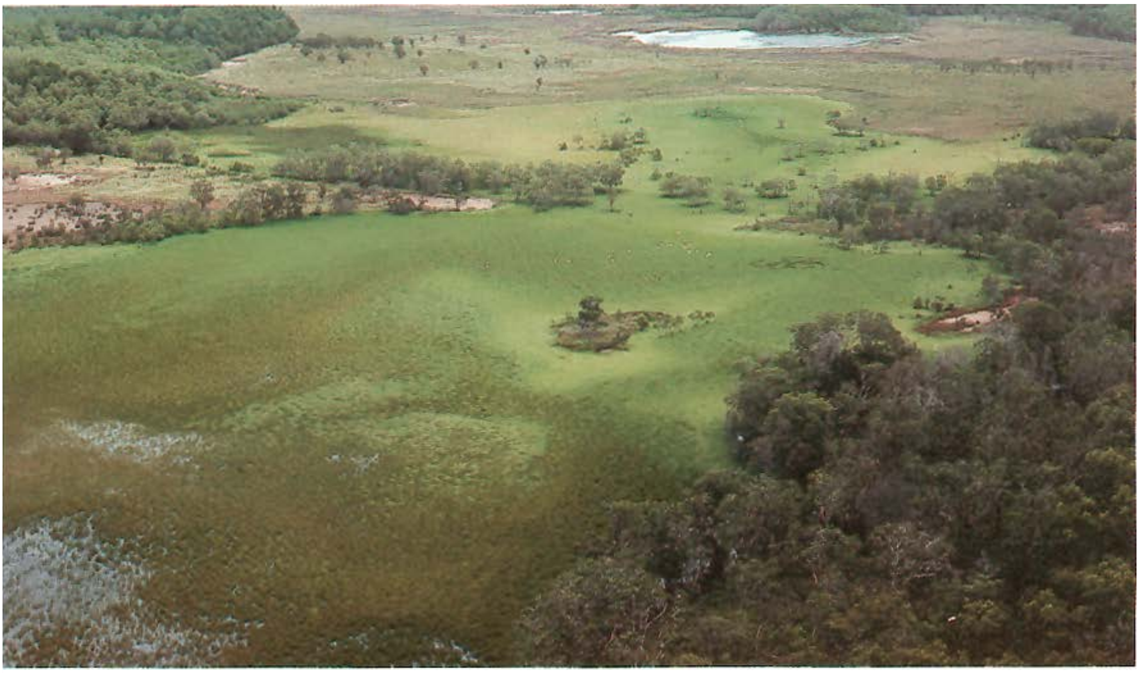

Figure 115. *Eleocharis dulcis* closed-sedgeland, mouth of Ducie River, Cape York Peninsula, Qld. Photograph — J.R.Clarkson.

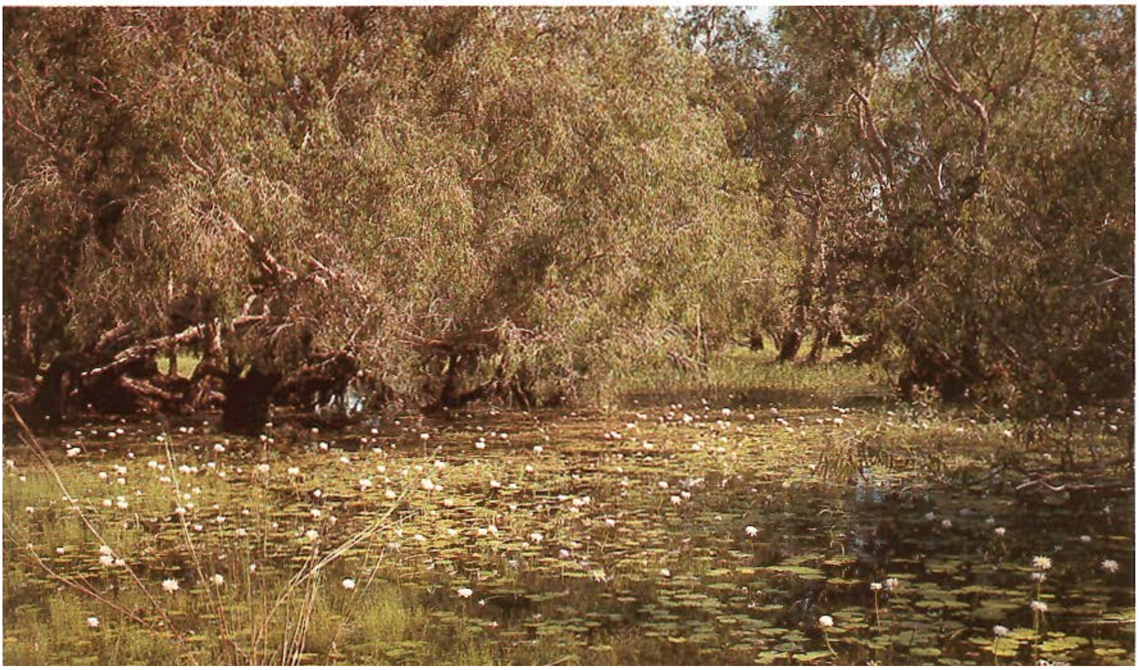

Figure 116. Billabong with *Nymphaea* spp. and marginal *Pandanus* sp., Island Billabong, Kakadu National Park, N.T.
Photograph — A.Wells.

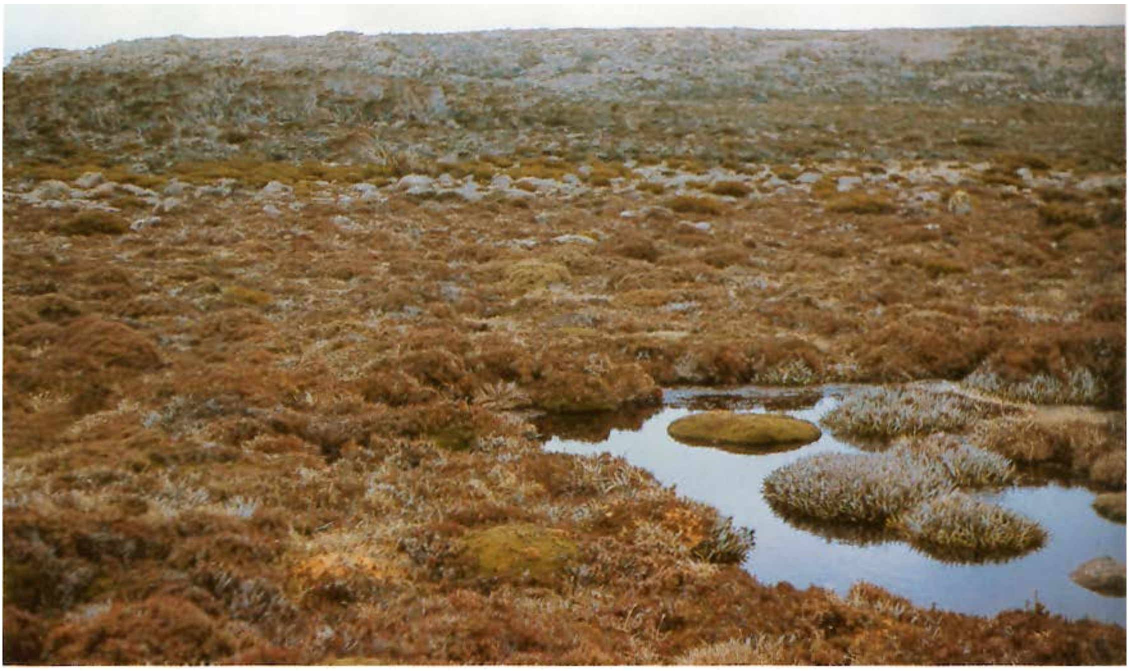

Figure 117. Wet alpine heath, with *Abrotanella forsterioides*, *Astelia alpina* and *Richea sprengelioides*, Mt Wellington, Tas. Photograph — M.E.Phillips (ANBG).

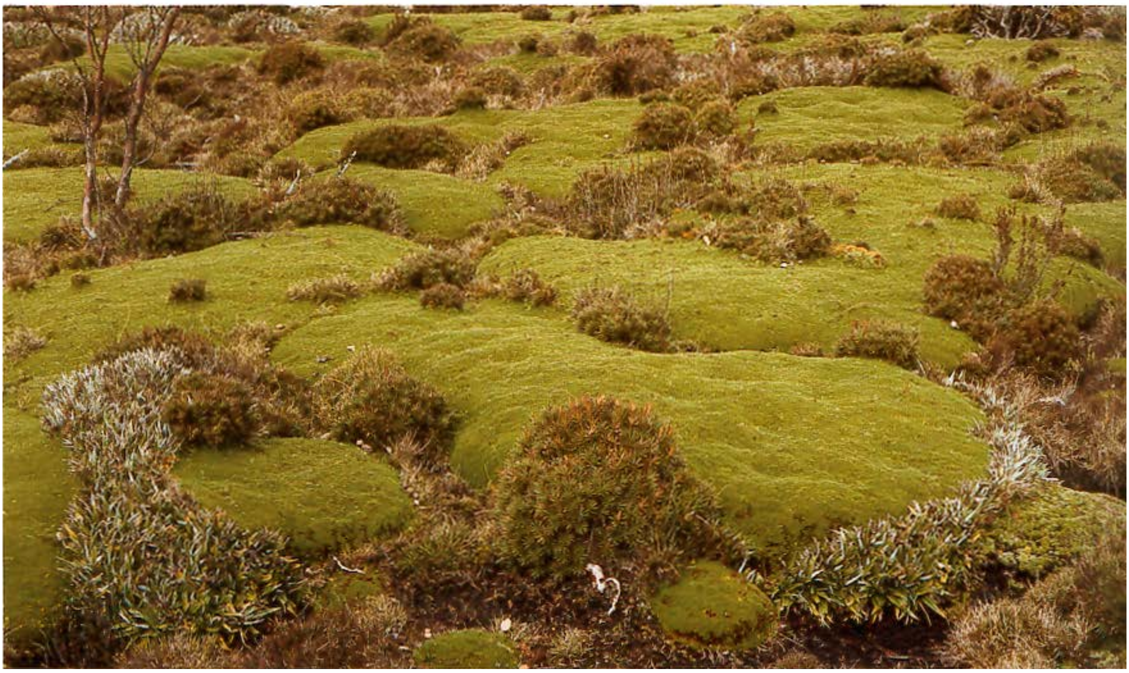

Figure 118. Bolster moor dominated by *Abrotanella forsterioides*, with *Astelia alpina* and *Richea scoparia*, Split Rock, Tas.
Photograph — S.J.Jarman.

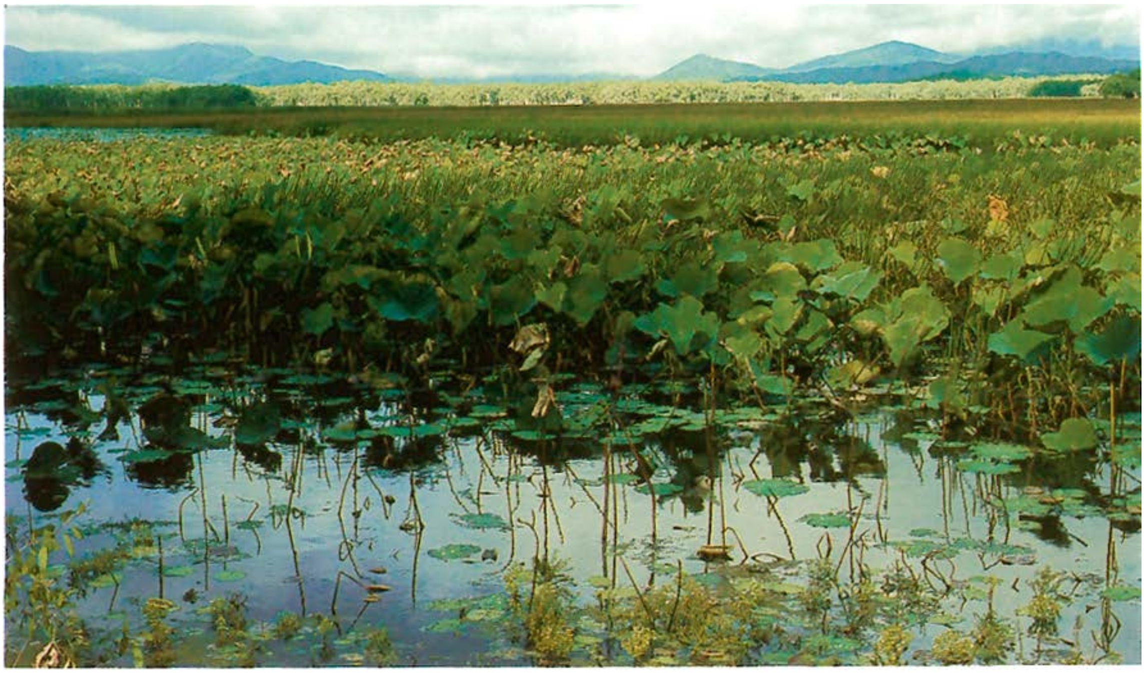

Figure 119. *Nelumbo nucifera* with *Nymphaea* sp. in shallower water, Kings Plains Lake, south-east of Cooktown, Qld. Photograph — M.D.Crisp.

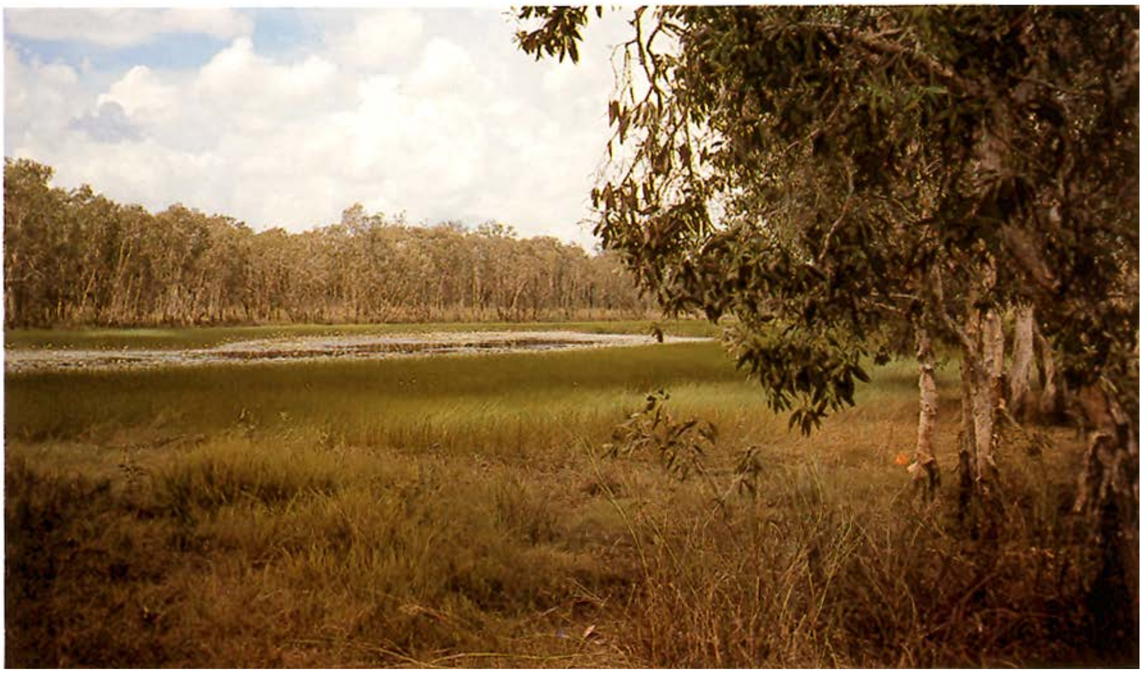

Figure 120. Billabong with fringing *Melaleuca leucodendron* forest, *Nymphaea* spp. and *Eleocharis* spp., Georgetown Billabong, N.T.
Photograph — A.Wells.

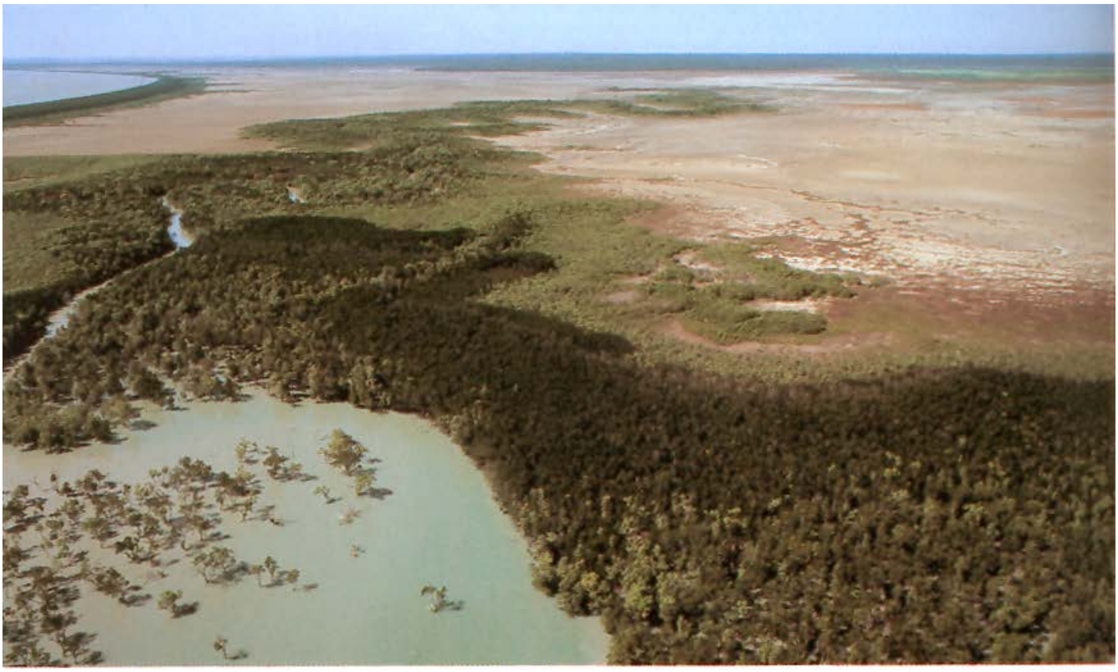

Figure 121. Mangrove forest with samphire swamp behind, near Point Farewell, mouth of East Alligator River, N.T. Photograph — C.Totterdell (ANBG).

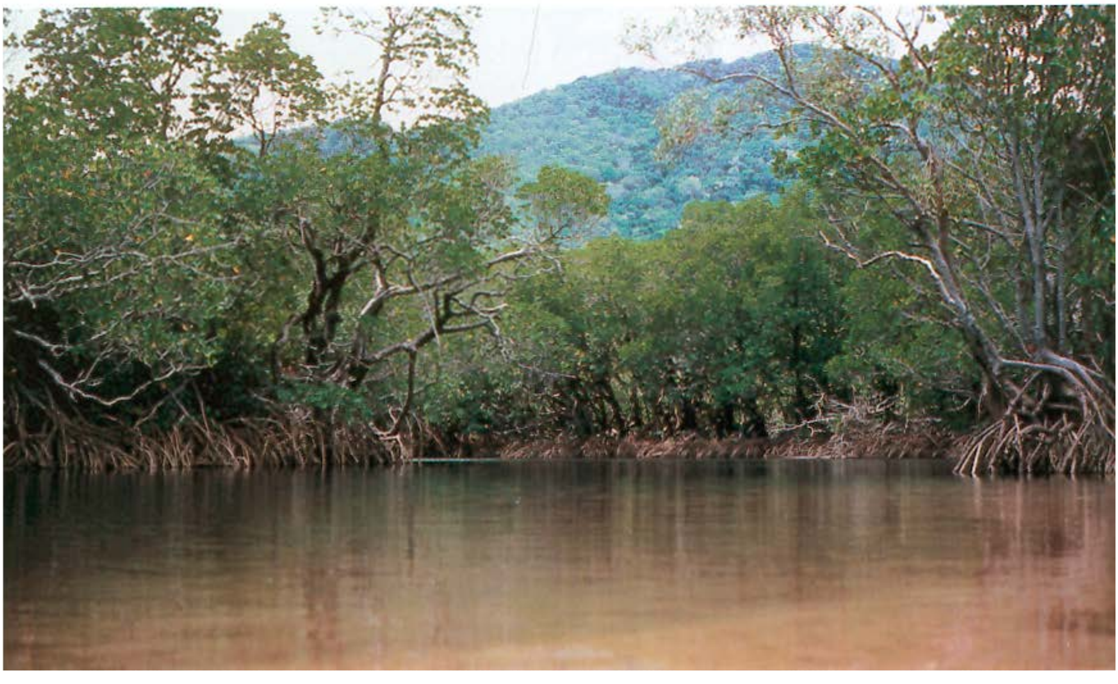

Figure 122. Mangrove forest, Cooktown, Qld. Photograph — G.Butler (ANBG).

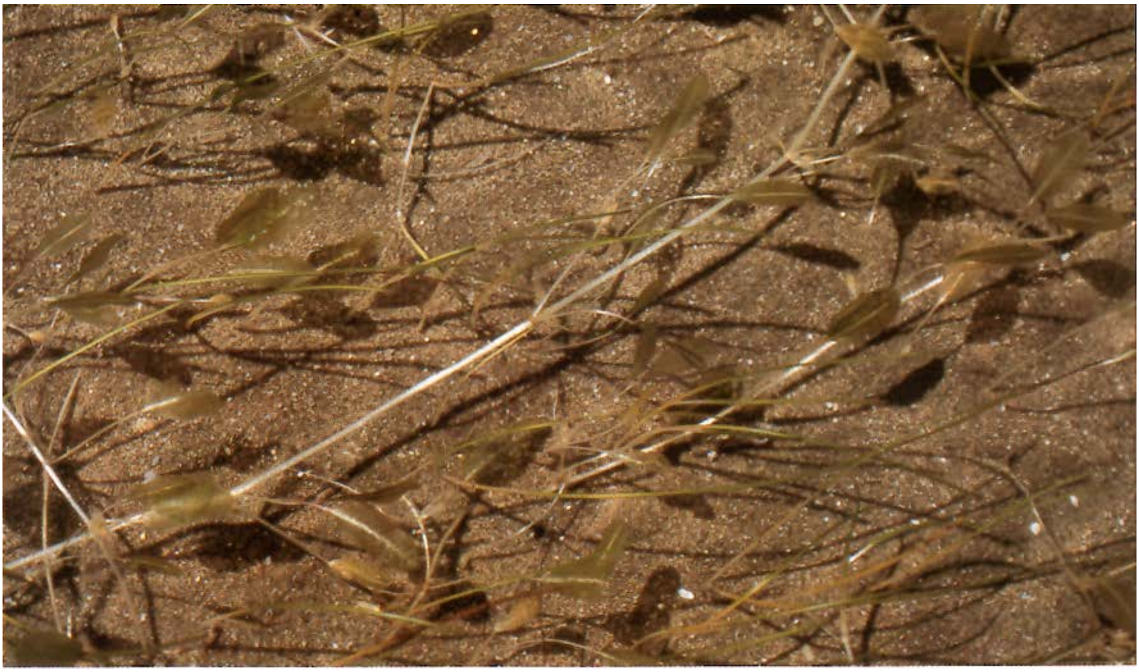

Figure 123. Seagrass bed, *Halophila ovalis* and *Halodule uninervis*, intertidal mudflats, Shelley Beach, Townsville, Qld. Photograph — M.Waycott.

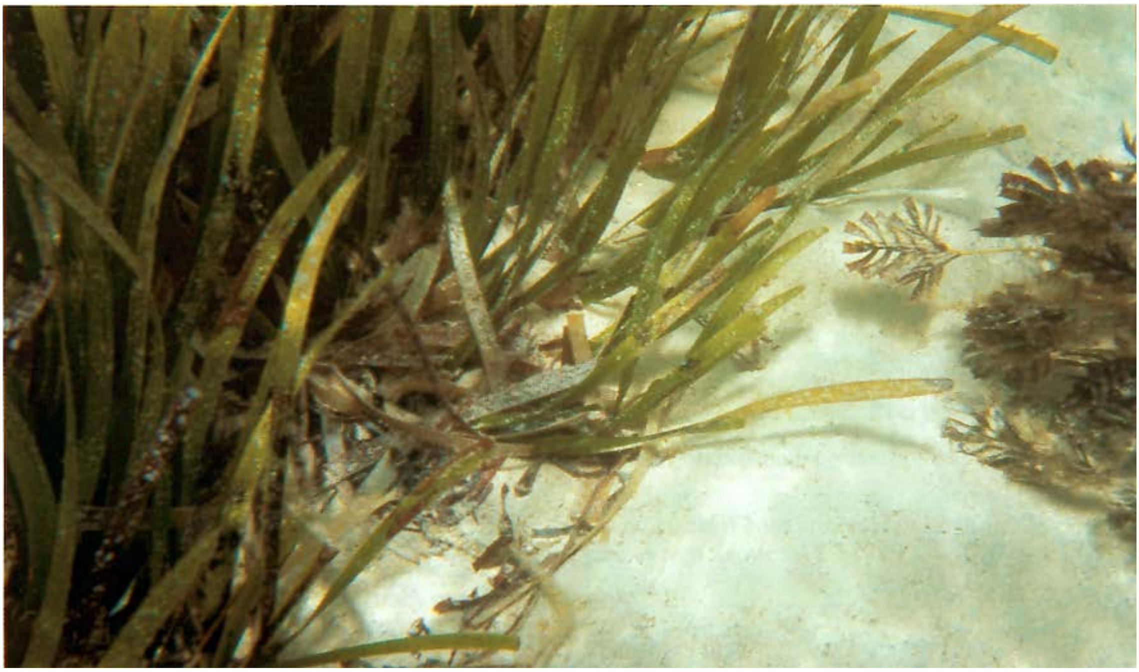

Figure 124. Seagrass bed, *Posidonia australis* and *Amphibolus antarctica*, near Rockingham, W.A.
Photograph — M.Waycott.

KEY TO FAMILIES OF FLOWERING PLANTS

A.E.Orchard[1]

This key is based on an unpublished key to Queensland flowering plants by the late A.Cayzer. It was modified and published as *Keys to the Families and Genera of Queensland Flowering Plants (Magnoliophyta)*, 2nd edn by H.T.Clifford & G.Ludlow (University of Queensland Press, 1978) and was further modified by H.T.Clifford for publication in *Flora of Australia Volume 1, Introduction*, 1st edn (Australian Government Publishing Service, 1981). In this edition it has again been modified and restructured, based on suggestions from numerous users over the last 15 years. Their contributions are gratefully acknowledged.

1 Embryo with 2 (rarely 1, 3 or more) cotyledons; leaf venation usually reticulate; leaf base rarely sheathing; perianth 4- or 5- (rarely 3- or more than 5-) merous (Dicotyledons)........2

1: Embryo with 1 cotyledon; leaf venation usually convergent; leaf base usually sheathing; perianth 3- (occasionally 2- or 4-) merous (Monocotyledons)....................................1010

Dicotyledons

2 Flowers with at least one perianth whorl *(1)*..3

2: Flowers lacking perianth...992

3 Either one or both perianth whorls fused into a cap *(2)* 4

3: Perianth segments not fused into a cap...10

4 Leaves invested with peltate scales *(3)*... **Himantandraceae**

4: Leaves glabrous or, if indumentum present, not of peltate scales 5

5 Leaves gland-dotted *(4:)*.. **Myrtaceae**

5: Leaves not gland-dotted...6

6 Leaf base sheathing *(5:)*..**Epacridaceae**

6: Leaf base not sheathing 7

7 Leaves exstipulate *(6:)*... **Eupomatiaceae**

7: Leaves stipulate..8

8 Tendrils present *(7:)* ....**Vitaceae**

8: Tendrils absent..9

9 Gynophore present; leaves usually alternate *(8:)* ....**Capparaceae**

9: Gynophore absent; leaves opposite ....**Eucryphiaceae**

10 Perianth segments more than 6 (counting sepals and petals if both present) or calyx cuplike and unlobed, with 5 or more petals *(3:)* 11

10: Perianth segments 6 or fewer (counting sepals and petals if both present, but not counting the bracts, scales or plumes of the pappus in Asteraceae)..........................693

11 Corolla segments (or perianth segments) free *(10)*...12

11: Corolla segments (or perianth segments) united 459

12 All or most flowers unisexual *(11)* 13

12: Most flowers bisexual..48

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[1] Australian Biological Resources Study, GPO Box 636, Canberra, Australian Capital Territory 2601.

13 Ovary superior *(12)* 14
13: Ovary inferior 44

14 Floating aquatics; leaves whorled, much divided *(13)* .... **Ceratophyllaceae**
14: Land plants; leaves alternate, opposite, or absent 15

15 Gynoecium apocarpous *(14:)* 16
15: Gynoecium syncarpous or carpel 1 19

16 Climbers or ramblers *(15)* 17
16: Non-climbers, not spreading 18

17 Climbers; leaves opposite *(16)* .... **Rutaceae**
17: Climbers (or plants spreading over the ground); leaves alternate .... **Menispermaceae**

18 Leaves gland-dotted *(16:)* .... **Rutaceae**
18: Leaves not gland-dotted .... **Simaroubaceae**

19 Leaves compound *(15:)* 20
19: Leaves simple or absent 26

20 Petals 4 *(19)* 21
20: Petals 5 23

21 Leaves gland-dotted *(20)* .... **Rutaceae**
21: Leaves not gland-dotted 22

22 Stamens 3–5 in male flowers *(21:)* .... **Simaroubaceae**
22: Stamens usually 8 in male flowers .... **Anacardiaceae**

23 Stamens 5 in male flowers *(20:)* .... **Anacardiaceae**
23: Stamens more than 5 in male flowers 24

24 Stamens usually 8; style 1; stigma entire or lobed *(23:)* .... **Sapindaceae**
24: Stamens 10; styles or stigmas more than 1 25

25 Ovary entire; stigmas glabrous *(24:)* .... **Anacardiaceae**
25: Ovary lobed; stigmas plumose .... **Simaroubaceae**

26 Leaves opposite *(19:)* 27
26: Leaves alternate, clustered, or absent 28

27 Flowers strictly unisexual; shrubs or trees *(26)* .... **Euphorbiaceae**
27: Flowers polygamous; trees usually with yellow sap .... **Clusiaceae**

28 Climbers with tendrils *(26:)* .... **Passifloraceae**
28: Tendrils absent 29

29 Twiners or lianes *(28:)* 30
29: Shrubs, trees or herbs, sometimes scrambling 31

30 Stipules absent; disc absent; petals smaller than sepals, entire, sometimes absent *(29)* .... **Menispermaceae**
30: Stipules present; disc present; petals as long as or longer than sepals, emarginate .... **Dichapetalaceae**

31 Latex present *(29:)* .... **Euphorbiaceae**
31: Latex absent 32

32 Styles more than 3 *(31:)* .... **Malvaceae**
32: Styles 1–3 or stigmas sessile 33

33 Styles 3, distinct, simple or branched *(32:)* .... **Euphorbiaceae**
33: Style 1 or absent (stigma sessile) 34

34 Style 1 with 2 or more stigmas *(33:)* 35
34: Style and stigma 1 or stigma sessile 39

35 Male flowers with staminodes *(34)* .... **Tiliaceae**
35: Male flowers without staminodes 36

36 Ovary 1-locular *(35:)* .... **Flacourtiaceae**
36: Ovary more than 1-locular 37

37 Fruit a succulent drupe; leaves succulent; seeds non-endospermic *(36:)* **Zygophyllaceae**
37: Fruit dry; leaves not succulent though often thick; seeds endospermic 38

38 Carpels dry, falling entire; stamens fused into a column *(37:)* .... **Malvaceae**
38: Carpels dry, dehiscent; stamens free or solitary .... **Euphorbiaceae**

39 Calyx segments free *(34:)* .... **Euphorbiaceae**
39: Calyx segments united or calyx minute 40

40 Ovary 1-locular *(39:)* 41
40: Ovary more than 1-locular 43

41 Ovary stipitate *(40)* .... **Capparaceae**
41: Ovary sessile 42

42 Leaves stipulate *(41:)* .... **Malvaceae**
42: Leaves exstipulate .... **Icacinaceae**

43 Leaves not succulent; trees; flowers usually unisexual, dioecious; seeds endospermic *(40:)* .... **Aquifoliaceae**
43: Leaves succulent; shrubs, subshrubs or herbs; flowers bisexual; seeds non-endospermic .... **Zygophyllaceae**

44 Climber with tendrils *(13:)* .... **Cucurbitaceae**
44: Non-climbers 45

45 Herbs or undershrubs *(44:)* 46
45: Trees 47

46 Petals 5 *(45)* .... **Apiaceae**
46: Petals 0, 2 or 4 .... **Haloragaceae**

47 Style 1 *(45:)* .... **Hernandiaceae**
47: Styles 2 or more .... **Datiscaceae**

48 Gynoecium apocarpous *(12:)* 49
48: Gynoecium syncarpous or carpel 1 88

49 Flowers perigynous *(48)* 50
49: Flowers hypogynous 53

50 Leaves alternate or radical *(49)* 51
50: Leaves opposite 52

51 Sepals 5; stamens numerous *(50)* .... **Rosaceae**
51: Sepals 4; stamens 4 or 8 .... **Crassulaceae**

52 Perianth segments numerous; carpels numerous *(50:)* .... **Idiospermaceae**
52: Sepals 4 or 5; petals 4 or 5; carpels 4 .... **Crassulaceae**

53 Stamens numerous *(49:)* 54
53: Stamens 10 or fewer 66

54 Leaves peltate *(53)* 55
54: Leaves not peltate 56

55 Carpels embedded in receptacle *(54)* .... **Nelumbonaceae**
55: Carpels not embedded in receptacle .... **Cabombaceae**

56 Style 1 with 3–5 stigmas *(54:)* .... **Ochnaceae**
56: Styles (or stigmas when styles much reduced) as many as carpels 57

57 Climbers *(56:)* 58
57: Non-climbers 60

58 Perianth of tepals; perianth segments 10–14 *(57)* .... **Austrobaileyaceae**
58: Perianth of distinct sepals and petals 59

59 Sepals 3; petals 6 *(58:)* .... **Annonaceae**
59: Sepals 4 or 5; petals 3–5 .... **Dilleniaceae**

60 Perianth segments all petaloid *(57:)* 61
60: One or more whorls of perianth sepaloid 62

61 Herbs *(60)* .... **Ranunculaceae**
61: Shrubs or trees .... **Magnoliaceae**

62 Leaves with peltate indumentum; perianth spiral *(60:)* .... **Himantandraceae**
62: Indumentum, if present, not peltate 63

63 Perianth in 3 whorls of 3 tepals *(62:)* .... **Annonaceae**
63: Sepals 5; petals 5 64

64 Leaves bipinnate; trees *(63:)* .... **Mimosaceae**
64: Leaves simple, entire to incised 65

65 Herbs; leaves usually much incised *(64:)* .... **Ranunculaceae**
65: Trees, shrubs, or undershrubs; leaves entire to distinctly incised .... **Dilleniaceae**

66 Style 1; stigmas 1 or more *(53:)* 67
66: Styles (or stigmas when styles much reduced) free from one another, as many as there are carpels 72

67 Leaves peltate *(66)* .... **Tropaeolaceae**
67: Leaves not peltate 68

68 Leaves gland-dotted *(67:)* .... **Rutaceae**
68: Leaves not gland-dotted 69

69 Leaves alternate *(68:)* 70
69: Leaves opposite 71

70 Stigma simple *(69)* .... **Ochnaceae**
70: Stigmas 3 or more .... **Simaroubaceae**

71 Flowers 4-merous *(69:)* .... **Rutaceae**
71: Flowers 5-merous .... **Malpighiaceae**

72 Leaves compound *(66:)* 73
72: Leaves simple or absent 74

73 Leaves gland-dotted *(72)* .... **Rutaceae**
73: Leaves not gland-dotted .... **Simaroubaceae**

74 Leaves opposite *(72:)* 75
74: Leaves alternate, radical, clustered, or absent 77

75 Sepals 4; petals 4 *(74)* .... **Crassulaceae**
75: Sepals 5; petals 5 76

76 Petals sessile or with short claws; leaves fleshy *(75:)* .... **Crassulaceae**
76: Petals with long claws; leaves not fleshy .... **Malpighiaceae**

77 Flowers 3-merous (usually sepals 6, petals 6, carpels 6 or 3) *(74:)* .... **Menispermaceae**
77: Flowers 4- or 5-merous 78

78 Flowers 4-merous *(77:)* 79
78: Flowers 5-merous 80

79 Leaves fleshy; seeds lacking endosperm *(78)* .... **Crassulaceae**
79: Leaves not fleshy; seeds endospermic .... **Saxifragaceae**

80 Stamens united into one or more groups *(78:)* 81
80: Stamens free 82

81 Carpels 2 *(80)* .... **Dilleniaceae**
81: Carpels 3 .... **Malpighiaceae**

82 Leaves not expanded at time of flowering *(80:)* .... **Anacardiaceae**
82: Leaves present at time of flowering 83

83 Leaves lobed or much dissected *(82:)* .... **Ranunculaceae**
83: Leaves entire 84

84 Carpels more than 5 *(83:)* .... **Ranunculaceae**
84: Carpels 5 or fewer 85

85 Leaves fleshy *(84:)* .... **Crassulaceae**
85: Leaves not fleshy 86

86 Carpels usually 2 or 3 *(85:)* .... **Dilleniaceae**
86: Carpels 5 87

87 Leaves stipulate; petals white *(86:)* .... **Simaroubaceae**
87: Leaves exstipulate; petals yellow .... **Surianaceae**

88 Petals 2–4 *(48:)* 89
88: Petals 5 or more, or whole perianth petaloid or sepaloid 91

89 Petals 2 *(88)* .... **Polygalaceae**
89: Petals 3 or 4 90

90 Petals 3 *(89:)* 92
90: Petals 4 94

91 Petals 5 *(88:)* 176
91: Petals more than 5, or whole perianth petaloid or sepaloid, sometimes in 1 whorl 416

92 Leaves compound *(90)* .... **Caesalpiniaceae**
92: Leaves simple 93

93 Sepals 5 *(92:)* .... **Polygalaceae**
93: Sepals 4 .... **Zygophyllaceae**

94 Sepals 5 or 6 *(90:)* 95
94: Sepals 4, rarely 2 or 3 96

95 Sepals 5 *(94)* 167
95: Sepals 6 174

96 Ovary superior *(94:)* 97
96: Ovary inferior 151

97 Leaves radical or alternate *(96)* 98
97: Leaves opposite or verticillate 125

98 Styles more than 1, quite free from one another *(97)* .... **Droseraceae**
98: Style 1, with 1 or more stigmas, or stigma sessile 99

99 Stamens 2–4 *(98:)* 100
99: Stamens 6 or more 109

100 Stamens 2 or 3 *(99)* 101
100: Stamens 4 or 5 103

101 Stamens 3 *(100)* .... **Caesalpiniaceae**
101: Stamens 2 102

102 Leaves simple, entire or much divided *(101:)* .... **Brassicaceae**
102: Leaves compound .... **Caesalpiniaceae**

103 Stamens opposite petals *(100:)* 104
103: Stamens alternating with petals 105

104 Placentation basal or free-central *(103)* .... **Myrsinaceae**
104: Placentation parietal .... **Brassicaceae**

105 Climbers with leaf-opposed tendrils *(103:)* .... **Vitaceae**
105: Plants without tendrils 106

106 Leaves compound *(105:)* .... **Capparaceae**
106: Leaves simple or absent 107

107 Herbs *(106:)* .... **Brassicaceae**
107: Shrubs or trees 108

108 Leaves with short, pointed lobes *(107:)* .... **Aquifoliaceae**
108: Leaves quite entire .... **Celastraceae**

109 Stamens 6–8 *(99:)* 110
109: Stamens 10 or more 121

110 Stamens 6 *(109)* 111
110: Stamens 7 or 8 113

111 Stamens tetradynamous; leaves simple *(110)* .... **Brassicaceae**
111: Stamens not tetradynamous 112

112 Leaves apparently cuneate and 2-lobed, in connate pairs in upper stem *(111:)* .... **Zygophyllaceae**
112: Leaves palmately dissected, alternate .... **Capparaceae**

113 Stamens united *(110:)* .... **Meliaceae**
113: Stamens free 114

114 Leaves simple or absent *(113:)* 115
114: Leaves compound 117

115 Leaves dissected *(114)* .... **Sapindaceae**
115: Leaves entire or absent 116

116 Petals glabrous *(115:)* .... **Tremandraceae**
116: Petals densely hairy inside .... **Olacaceae**

117 Leaves 3-foliolate or palmate *(114:)* 118
117: Leaves pinnate 120

118 Ovules numerous in each loculus *(117)* .... **Capparaceae**
118: Ovules 1 or 2 in each loculus 119

119 Ovules 1 in each loculus *(118:)* .... **Simaroubaceae**
119: Ovules 2 in each loculus .... **Burseraceae**

120 Ovules 1 in each loculus *(117:)* .... **Sapindaceae**
120: Ovules 2 in each loculus .... **Burseraceae**

121 Flowers in heads or spikes; heads solitary or in racemes *(109:)* .... **Mimosaceae**
121: Flowers not in heads or spikes 122

122 Ovary borne on long stalk (gynophore) *(121:)* .... **Capparaceae**
122: Ovary sessile 123

123 Ovary 1-locular *(122:)* .... **Flacourtiaceae**
123: Ovary more than 1-locular 124

124 Anthers opening by longitudinal slits; fruit dry, breaking into cocci or mericarps (capsule in *Peganum*) *(123:)* .... **Zygophyllaceae**
124: Anthers opening by terminal pores; fruit a drupe or capsule .... **Elaeocarpaceae**

125 Leaves large, palmately lobed *(97:)* .... **Aceraceae**
125: Leaves otherwise 126

126 Stamens 2 or 4 *(125:)* 127
126: Stamens 5 or more 135

127 Stamens 2 *(126)* 128
127: Stamens 4 129

128 Flowers in clusters, racemes, or panicles *(127)* .... **Oleaceae**
128: Flowers solitary in leaf axils .... **Lythraceae**

129 Leaves gland-dotted *(127:)* 130
129: Leaves not gland-dotted 131

130 Style and stigma 1 *(129)* .... **Rutaceae**
130: Styles or stigmas 4 .... **Cunoniaceae**

131 Stamens perigynous *(129:)* 132
131: Stamens hypogynous 133

132 Anthers opening by pores; anther-connective with sickle-shaped appendages *(131)* .... **Melastomataceae**
132: Anthers opening longitudinally; connective without appendages .... **Lythraceae**

133 Styles 4 *(131:)* .... **Elatinaceae**
133: Style 1 134

134 Trees, shrubs or climbers; leaves simple or scale-like *(133:)* .... **Celastraceae**
134: Annual herb; leaves 2-lobed .... **Zygophyllaceae**

135 Stamens 5–8 *(126:)* 136
135: Stamens 10 or numerous 148

136 Leaves simple or absent *(135)* 137
136: Leaves compound 146

137 Leaves 2-lobed *(136)* .... **Zygophyllaceae**
137: Leaves entire, or with more than 2 lobes 138

138 Leaves gland-dotted *(137:)* .... **Rutaceae**
138: Leaves not gland-dotted 139

139 Ovary half-inferior; margins of petals fringed with long hairs *(138:)* ..... **Rhizophoraceae**
139: Ovary wholly superior; petals not fringed 140

140 Style and stigma 1 *(139:)* 141
140: Styles or stigmas more than 1 145

141 Perianth hypogynous *(140)* 142
141: Perianth perigynous 144

142 Leaves in whorls of 3 or 4 *(141)* ..... **Tremandraceae**
142: Leaves in pairs, opposite 143

143 Fruits not winged; subshrubs, shrubs, or trees *(142:)* ..... **Rutaceae**
143: Fruits winged; subshrubs ..... **Zygophyllaceae**

144 Leaves with 2 or more conspicuous longitudinal veins besides midrib *(141:)* ..... **Melastomataceae**
144: Midrib only conspicuous longitudinal vein ..... **Lythraceae**

145 Leaves with revolute margins; style 1, with 3 branches *(140:)* ..... **Frankeniaceae**
145: Leaf margins not revolute; styles 2 or 4 ..... **Cunoniaceae**

146 Stamens united *(136:)* ..... **Meliaceae**
146: Stamens free 147

147 Leaves gland-dotted, usually with several leaflets *(146:)* ..... **Rutaceae**
147: Leaves not gland-dotted, with only 2 leaflets ..... **Zygophyllaceae**

148 Flowers hypogynous, polygamous *(135:)* 149
148: Flowers perigynous 150

149 Stipules absent *(148)* ..... **Clusiaceae**
149: Stipules present ..... **Eucryphiaceae**

150 Style and stigma 1 *(148:)* ..... **Lythraceae**
150: Styles more than 1 ..... **Cunoniaceae**

151 Leaves gland-dotted *(96:)* ..... **Myrtaceae**
151: Leaves not gland-dotted 152

152 Stamens numerous *(151:)* 153
152: Stamens 10 or fewer 154

153 Style and stigma 1 *(152)* ..... **Lecythidaceae**
153: Style with 4 stigmas ..... **Grossulariaceae**

154 Leaves alternate or radical *(152:)* 155
154: Leaves opposite or verticillate 161

155 Style 1, with 1 or more stigmas *(154)* 156
155: Styles several, free 160

156 Aquatic herbs with alternate, rosetted floating leaves and opposite submerged leaves *(155)* ..... **Trapaceae**
156: Trees, shrubs or herbs 157

157 Stigmas 2 or 4 *(156:)* 158
157: Stigma 1 159

158 Stigmas 2 *(157)* .... **Alangiaceae**
158: Stigmas 4 .... **Onagraceae**

159 Ovary 1-locular *(157:)* .... **Combretaceae**
159: Ovary 4-locular .... **Onagraceae**

160 Herbs; flowers very small *(155:)* .... **Haloragaceae**
160: Shrubs or trees; flowers greater than 6 mm in diameter .... **Grossulariaceae**

161 Styles several, free *(154:)* .... **Haloragaceae**
161: Style 1, with 1 or more stigmas 162

162 Petals fringed with long hairs *(161:)* .... **Rhizophoraceae**
162: Petals not fringed 163

163 Stamens 4 *(162:)* 164
163: Stamens more than 4, usually 8 165

164 Aquatic herbs *(163)* .... **Trapaceae**
164: Shrubs .... **Grossulariaceae**

165 Leaves with 2 or more longitudinal veins besides midrib *(163:)* .... **Melastomataceae**
165: Midrib the only longitudinal vein 166

166 Ovary 1-locular *(165:)* .... **Melastomataceae**
166: Ovary 4-locular .... **Onagraceae**

167 Ovary 1- or 2-locular *(95)* 168
167: Ovary 3–5-locular 171

168 Ovary adnate to one side of calyx tube *(167)* .... **Chrysobalanaceae**
168: Ovary free 169

169 Fruit indehiscent, globose *(168:)* .... **Xanthophyllaceae**
169: Fruit dehiscent, a legume or capsule 170

170 Fruit a legume *(169:)* .... **Caesalpiniaceae**
170: Fruit a capsule .... **Zygophyllaceae**

171 Ovary usually 3-locular *(167:)* 172
171: Ovary 4- or 5-locular 173

172 Style 1; ovary 3-locular *(171)* .... **Zygophyllaceae**
172: Styles usually 2 or more (if style 1, then ovary 1-locular) .... **Sapindaceae**

173 Ovary 4-locular *(171:)* .... **Elaeocarpaceae**
173: Ovary 5-locular .... **Meliaceae**

174 Ovary open at top, with sessile stigmas *(95:)* .... **Resedaceae**
174: Ovary not open at top 175

175 Herbs *(174:)* .... **Lythraceae**
175: Small shrubs .... **Saxifragaceae**

176 Sepals 2 or 3 *(91)* 177
176: Sepals 4 or more 186

177 Sepals 2 *(176)* 178
177: Sepals 3 182

178 Flowers zygomorphic *(177)* .... **Caesalpiniaceae**
178: Flowers actinomorphic 179

179 Twiners *(178:)* .... **Basellaceae**
179: Non-twiners 180

180 Shrubs or trees *(179:)* .... **Lecythidaceae**
180: Herbs 181

181 Stamens 5 or fewer; perianth often scarious *(180:)* .... **Amaranthaceae**
181: Stamens usually more than 5; perianth not scarious; leaves (and often stems) fleshy .... **Portulacaceae**

182 Leaves compound *(177:)* .... **Caesalpiniaceae**
182: Leaves simple or absent 183

183 Leaf venation palmate *(182:)* .... **Caesalpiniaceae**
183: Leaf venation not palmate 184

184 Stamens 5 *(183:)* .... **Hamamelidaceae**
184: Stamens 8 or more 185

185 Stamens 8 *(184:)* .... **Polygalaceae**
185: Stamens numerous .... **Lecythidaceae**

186 Sepals 4 *(176:)* 187
186: Sepals 5 or more, or calyx cup-like with indistinct lobes, or entire in bud 188

187 Stamens 8–10, free or united *(186)* .... **Caesalpiniaceae**
187: Stamens numerous, united .... **Lecythidaceae**

188 Ovary superior *(186:)* 189
188: Ovary inferior or semi-inferior 381

189 Style 1 with simple stigma, or stigma sessile *(188)* 190
189: Styles or stigmas more than 1 302

190 Leaves opposite or verticillate (rarely absent at flowering in some introduced deciduous species) *(189)* 191

190: Leaves alternate, radical, or absent 212

191 Leaves gland-dotted *(190)* 192
191: Leaves not gland-dotted 194

192 Leaves compound *(191)* .... **Rutaceae**
192: Leaves simple 193

193 Flowers hypogynous *(192:)* .... **Rutaceae**
193: Flowers perigynous or epigynous .... **Myrtaceae**

194 Leaves simple *(191:)* 195
194: Leaves compound 209

195 Leaves 2-lobed, ± succulent with obscure venation *(194)* .... **Zygophyllaceae**
195: Leaves not 2-lobed, with at least midrib apparent 196

196 Leaves with 2 or more conspicuous longitudinal veins besides midrib *(195:)* .... **Melastomataceae**
196: Midrib only conspicuous longitudinal vein 197

197 Stamens 10 or fewer *(196:)* 198
197: Stamens numerous 207

198 Flowers actinomorphic *(197)* 199
198: Flowers zygomorphic 205

199 Flowers perigynous *(198)* .... **Lythraceae**
199: Flowers not perigynous 200

200 Stamens 3 *(199:)* .... **Hippocrateaceae**
200: Stamens 5 or more 201

201 Stamens 5 *(200:)* .... **Celastraceae**
201: Stamens usually 10 202

202 Ovary half-inferior *(201:)* .... **Rhizophoraceae**
202: Ovary quite superior 203

203 Petals with narrow, pointed lobes *(202:)* .... **Rhizophoraceae**
203: Petals entire 204

204 Petals clawed; stamens unequal, usually united at base *(203:)* .... **Malpighiaceae**
204: Petals sessile, shorter than sepals .... **Rhizophoraceae**

205 Stamens 5, united; anthers connate around ovary *(198:)* .... **Violaceae**
205: Stamens 10 206

206 Ovary 1-locular; ovules 2 or more *(205:)* .... **Fabaceae**
206: Ovary 2- or 3-locular; 1 ovule in each loculus .... **Malpighiaceae**

207 Flowers perigynous *(197:)* .... **Lythraceae**
207: Flowers hypogynous 208

208 Ovary 1-locular *(207:)* .... **Mimosaceae**
208: Ovary 2 or more-locular .... **Elaeocarpaceae**

209 Stamens 5 *(194:)* .... **Meliaceae**
209: Stamens more than 5 210

210 Stamens united *(209:)* .... **Fabaceae**
210: Stamens free 211

211 Ovary 1-locular *(210:)* .... **Fabaceae**
211: Ovary 2- or more-locular .... **Zygophyllaceae**

212 Stamens 1–5 *(190:)* 213
212: Stamens 6 or more 219

213 Stamen 1 *(212)* 214
213: Stamens 2–5 215

214 Leaves deeply notched and palmately veined *(213)* .... **Caesalpiniaceae**
214: Leaves entire and pinnately veined .... **Anacardiaceae**

215 Stamens 2–4 *(213:)* 216
215: Stamens 5 221

216 Leaves simple *(215)* 217
216: Leaves pinnate or bipinnate 218

217 Leaf venation well-marked and palmate *(216)* .... **Caesalpiniaceae**
217: Leaf venation inconspicuous, or leaves absent .... **Olacaceae**

218 Stipules present; calyx oblique, of 5 segments; ovary 4- or 5-locular; fruit a capsule *(216:)* .... **Melianthaceae**
218: Stipules absent; calyx not oblique, of 5 free sepals; ovary 1-locular; fruit a legume .... **Caesalpiniaceae**

219 Stamens 10 or more *(212:)* 220
219: Stamens 6–9 (rarely 5–10) 254

220 Stamens 10 *(219)* 261
220: Stamens numerous 285

221 Leaves simple or absent *(215:)* 222
221: Leaves compound 245

222 Leaves bifid; venation palmate *(221)* .... **Caesalpiniaceae**
222: Leaves not bifid 223

223 Herbs *(222:)* 224
223: Shrubs, trees or woody climbers 227

224 Twiners *(223)* 225
224: Plants ±erect, not twining 226

225 Sap milky *(224)* .... **Cardiopteridaceae**
225: Sap not milky .... **Pittosporaceae**

226 Flowers actinomorphic *(224:)* .... **Byblidaceae**
226: Flowers zygomorphic .... **Violaceae**

227 Small shrubs; flowers zygomorphic *(223:)* .... **Violaceae**
227: Shrubs, trees or woody climbers; flowers actinomorphic or nearly so 228

228 Climbers *(227:)* 229
228: Non-climbers, ±erect 230

229 Twiners *(228)* .... **Pittosporaceae**
229: Climbers with leaf-opposed tendrils .... **Vitaceae**

230 Stamens opposite petals or tepals *(228:)* 231
230: Stamens alternate with petals or tepals 233

231 Each stamen ±enclosed by small hood-shaped petal *(230)* .... **Rhamnaceae**
231: Stamens not enclosed by petals 232

232 Fruit dehiscent (a capsule, follicle, samara or schizocarp), usually many-seeded (1 seed in *Waltheria*); ovules 2 per carpel *(231:)* .... **Sterculiaceae**
232: Fruit a 1-seeded drupe; ovule 1 per carpel .... **Opiliaceae**

233 Leaves gland-dotted *(230:)* .... **Rutaceae**
233: Leaves not gland-dotted 234

234 Base of calyx covered by several imbricate sepaloid bracteoles *(233:)* **Epacridaceae**
234: Bracteoles absent or not covering base of calyx 235

235 Sepals free *(234:)* 236
235: Sepals united 240

236 Ovary 3- or 5-locular *(235)* 237
236: Ovary 1- or 2-locular 238

237 Ovary 3-locular *(236)* .... **Celastraceae**
237: Ovary 5-locular .... **Grossulariaceae**

238 Ovules 1 per loculus *(236:)* .... **Corynocarpaceae**
238: Ovules 2–several per loculus 239

239 Ovary 1- or 2-locular; ovules few to many per loculus *(238:)* .... **Pittosporaceae**
239: Ovary 1-locular; ovules 2 .... **Icacinaceae**

240 Ovules 1 per ovary *(235:)* .... **Icacinaceae**
240: Ovules 2 or more per ovary 241

241 Ovary 1-locular *(240:)* 242
241: Ovary 2- or more-locular 243

242 Fruit 1-seeded *(241)* .... **Icacinaceae**
242: Fruit with 2–numerous seeds .... **Proteaceae**

243 Ovary subtended by nectar-secreting disc *(241:)* .... **Celastraceae**
243: Ovary not subtended by nectar-secreting disc 244

244 Style 1 *(243:)* .... **Pittosporaceae**
244: Styles 2 or more .... **Grossulariaceae**

245 Climbers with leaf-opposed tendrils *(221:)* .... **Vitaceae**
245: Non-climbers or, if climbing, tendrils not leaf-opposed or tendrils absent 246

246 Leaves gland-dotted *(245:)* .... **Rutaceae**
246: Leaves not gland-dotted 247

247 Stamens 5, staminodes 5 *(246:)* 248

247: Stamens 5, staminodes absent 250

248 Herbs; leaves 2-foliolate or pinnate; ovary with axile placentas; fruit usually with 2 or more seeds *(247)* .... **Zygophyllaceae**

248: Trees or woody climbers 249

249 Trees; leaves pinnate; ovary with 3 parietal placentas; fruit a long 3-angled capsule *(248:)* .... **Moringaceae**

249: Woody climbers; leaves imparipinnate; ovary with 2 collateral ovules; fruit 1-seeded .... **Connaraceae**

250 Stamens free *(247:)* 251

250: Stamens united 253

251 Ovary 1-locular; leaves bipinnate *(250)* .... **Mimosaceae**

251: Ovary 3–5-locular; leaves pinnate 252

252 Leaves exstipulate *(251:)* .... **Meliaceae**

252: Leaves stipulate .... **Zygophyllaceae**

253 Leaves pinnate *(250:)* .... **Meliaceae**

253: Leaves bi- or tripinnate .... **Vitaceae**

254 Stamens 9, united *(219:)* .... **Fabaceae**

254: Stamens free 255

255 Leaves simple *(254:)* 256

255: Leaves compound 258

256 Style arising from base of ovary *(255)* .... **Rosaceae**

256: Style terminal 257

257 Fruit a legume *(256:)* .... **Caesalpiniaceae**

257: Fruit globose .... **Xanthophyllaceae**

258 Ovary 1-locular, usually with more than 2 ovules *(255:)* .... **Caesalpiniaceae**

258: Ovary 2- or more-locular, with 1 or 2 ovules per loculus 259

259 Disc present; stamens inserted within disc *(258:)* .... **Sapindaceae**

259: Disc absent 260

260 Trees *(259:)* .... **Akaniaceae**

260: Herbs or shrubs .... **Zygophyllaceae**

261 Flowers zygomorphic *(220)* 262

261: Flowers actinomorphic or nearly so 263

262 Posterior petal enclosed by the remainder in bud, or absent *(261)* .... **Caesalpiniaceae**

262: Posterior petal enclosing the remainder in bud .... **Fabaceae**

263 Stamens united *(261:)* 264

263: Stamens free 269

264 Climbers *(263)* .... **Connaraceae**
264: Non-climbers... 265

265 Leaves 1–3-pinnate *(264:)* 266
265: Leaves simple... 267

266 Ovary 5-locular; leaves pinnate, bipinnate or tripinnate *(265)* .... **Meliaceae**
266: Ovary 1-locular; leaves bipinnate.. **Mimosaceae**

267 Staminal tube long and narrow, surrounding style *(265:)* .... **Meliaceae**
267: Staminal tube short, open 268

268 Ovary free; stipules persistent *(267:)* .... **Sterculiaceae**
268: Ovary adnate to one side of throat of calyx; stipules caducous ...... **Chrysobalanaceae**

269 Leaves simple or unifoliolate *(263:)* 270
269: Leaves compound... 276

270 Leaves gland-dotted *(269)* .... **Rutaceae**
270: Leaves not gland-dotted... 271

271 Style inserted near base of ovary, hairy *(270:)* .... **Simaroubaceae**
271: Style terminal... 272

272 Ovary and back of petals covered with scales; flowers in heads or clusters at end of branchlets *(271:)* .... **Rutaceae**
272: Not as above... 273

273 Flowers perigynous; ovary enclosed in hypanthium; stamens borne on hypanthium, sometimes near base *(272:)*.. **Lythraceae**
273: Flowers hypogynous; ovary and stamens not as above.............................. 274

274 Ovary usually stipitate; ovules several; sepals united *(273:)*............. **Caesalpiniaceae**
274: Ovary sessile; ovule 1 per locule.. 275

275 Fertile locule 1; stipules absent *(274:)* .... **Anacardiaceae**
275: Locules 5; stipules present.. **Ochnaceae**

276 Leaves gland-dotted *(269:)* .... **Rutaceae**
276: Leaves not gland-dotted... 277

277 Herbs *(276:)*.. **Zygophyllaceae**
277: Shrubs or trees 278

278 Leaves bipinnate *(277:)* .... **Mimosaceae**
278: Leaves pinnate.. 279

279 Leaflets 2; venation palmate *(278:)*.. **Caesalpiniaceae**
279: Leaflets more than 2 or, if 2, venation pinnate 280

280 Ovary 1-locular *(279:)*.. 281
280: Ovary 2- or more-locular 283

281 Stamens unequal; anthers dehiscing by pores *(280)*............................ **Caesalpiniaceae**
281: Stamens equal 282

282 Ovule 1 *(281:)* ... **Anacardiaceae**
282: Ovules more than 1 ... **Caesalpiniaceae**

283 Ovary 1- or 3-locular, with 1 ovule (rarely 2) per loculus *(280:)* ... **Sapindaceae**
283: Ovary 4- or 5-locular, with 2 ovules per loculus ... 284

284 Trees or large shrubs; fruit not angular *(283:)* ... **Burseraceae**
284: Small shrubs; fruit prominently angular ... **Zygophyllaceae**

285 Leaves gland-dotted *(220:)* ... 286
285: Leaves not gland-dotted ... 287

286 Flowers hypogynous *(285)* ... **Rutaceae**
286: Flowers perigynous or epigynous ... **Myrtaceae**

287 Leaves simple, reduced to phyllodes, or absent *(285:)* ... 288
287: Leaves compound ... 300

288 Stamens united into discrete groups *(287)* ... 289
288: Stamens free or only slightly united at base ... 290

289 Stamens united into 5 or 10 groups *(288)* ... **Tiliaceae**
289: Stamens united into a single group ... **Bombacaceae**

290 Flowers small, in globular heads or obloid or cylindrical spikes; stamens much exserted *(288:)* ... **Mimosaceae**
290: Flowers not as above; stamens usually not exserted ... 291

291 Flowers hypogynous *(290:)* ... 292
291: Flowers perigynous ... 298

292 Leaves fleshy, entire; shrubs *(291)* ... **Zygophyllaceae**
292: Leaves not fleshy, entire or divided: shrubs trees or climbers ... 293

293 Small trees; leaf lamina palmately divided into 5 or 7 lobes *(292:)* ... **Bixaceae**
293: Shrubs, trees or climbers; leaf margins entire, pinnately toothed or lobed ... 294

294 Calyx caducous *(293:)* ... **Bixaceae**
294: Calyx not caducous ... 295

295 Anthers dehiscing by terminal pores or slits *(294:)* ... **Elaeocarpaceae**
295: Anthers dehiscing longitudinally ... 296

296 Ovary 2- or more-locular *(295:)* ... **Tiliaceae**
296: Ovary 1-locular ... 297

297 Petals yellow, large *(296:)* ... **Dilleniaceae**
297: Petals not yellow, small ... **Flacourtiaceae**

298 Ovary adnate to one side of throat of calyx *(291:)* ... **Chrysobalanaceae**
298: Ovary free or completely adnate to calyx ... 299

299 Stamens inserted with petals at rim of hypanthium; ovules 1 or 2 in the ovary *(298:)* ...... **Rosaceae**
299: Stamens inserted on hypanthium below rim (sometimes almost at base); ovules usually numerous ...... **Lythraceae**

300 Leaves palmate *(287:)* ...... **Bixaceae**
300: Leaves pinnate or bipinnate 301

301 Petals valvate *(300:)* ...... **Mimosaceae**
301: Petals imbricate ...... **Caesalpiniaceae**

302 Leaves simple or absent *(189:)* 303
302: Leaves compound 368

303 Leaves opposite or verticillate *(302)* 304
303: Leaves alternate, radical, or absent 326

304 Stamens 10 or fewer *(303)* 305
304: Stamens indefinite 324

305 Styles or stigmas 5 *(304)* 306
305: Styles or stigmas less than 5 312

306 Leaves opposite *(305)* 307
306: Leaves verticillate 308

307 Leaves gland-dotted *(306)* ...... **Rutaceae**
307: Leaves not gland-dotted 309

308 Floating aquatic plants without roots *(306:)* ...... **Droseraceae**
308: Plants not aquatic ...... **Caryophyllaceae**

309 Styles 5, free *(307:)* 310
309: Style 1, with 5 stigmas 311

310 Ovary 1-locular *(309)* ...... **Caryophyllaceae**
310: Ovary 2–5-locular ...... **Elatinaceae**

311 Ovary 1-locular *(309:)* ...... **Caryophyllaceae**
311: Ovary 3- or more-locular ...... **Geraniaceae**

312 Leaves palmately lobed *(305:)* ...... **Aceraceae**
312: Leaves otherwise 313

313 Styles free *(312:)* 314
313: Styles united; stigmas 2 or more 318

314 Climbers or twiners *(313)* ...... **Malpighiaceae**
314: Non-climbers, non-twiners 315

315 Leaves gland-dotted *(314:)* ...... **Clusiaceae**
315: Leaves not gland-dotted 316

316 Mostly herbs; stems usually swollen at nodes *(315:)* ...... **Caryophyllaceae**
316: Shrubs or trees; nodes not swollen 317

317 Petals much more than 2 mm long, distinctly clawed *(316:)* .... **Malpighiaceae**
317: Petals scarcely 2 mm long, sessile or nearly so.. **Cunoniaceae**

318 Herbs, non-climbers, non-twiners *(313:)*..**Caryophyllaceae**
318: Shrubs, trees, climbers or twiners 319

319 Stamens 3 *(318:)* ....**Hippocrateaceae**
319: Stamens 5 or more...320

320 Stamens 10 *(319:)* .... **Malpighiaceae**
320: Stamens 5 or 6..321

321 Stamens opposite to and enclosed in petals *(320:)*...................................... **Rhamnaceae**
321: Stamens opposite sepals 322

322 Petals clawed, the claws cohering in an angular tube *(321:)* .... **Frankeniaceae**
322: Petals sessile or if clawed, the claws free 323

323 Petals sessile; stamens 5 *(322:)*.. **Celastraceae**
323: Petals clawed; stamens usually more than 5 .... **Malpighiaceae**

324 Leaves in whorls of six *(304:)* .... **Cunoniaceae**
324: Leaves opposite..325

325 Juice resinous; stipules absent *(324:)*... **Clusiaceae**
325: Juice not resinous; stipules present .... **Cistaceae**

326 Stamens united, often forming a conspicuous staminal tube *(303:)*........................327
326: Stamens free or arising from margin of a small disc 339

327 Styles 2 or more, free *(326)* 328
327: Style 1, with 2 or more stigmas..333

328 Stamens 8 *(327)*..**Aizoaceae**
328: Stamens 5, 10, or numerous 329

329 Climbers *(328:)* .... **Linaceae**
329: Non-climbers...330

330 Leaves often dentate or lobed, with stellate hairs *(329:)*..331
330: Leaves entire, glabrous 332

331 Stamens 15 or more, always united into a tube surrounding the ovary; anthers 1-celled; epicalyx often present *(330)*..**Malvaceae**
331: Stamens 5, 10, 15 or 20–30, free or sometimes united; anthers 2-celled; epicalyx never present .... **Sterculiaceae**

332 Stamens 10 *(330:)* ....**Erythroxylaceae**
332: Stamens 4 or 5... **Linaceae**

333 Petals attached to base of staminal tube; staminal tube usually long; stamens usually indefinite (rarely 10 or fewer); stigmas 3–5; shrubs *(327:)* ....**Malvaceae**
333: Not as above...334

334 Style branches (or stigmas) 2 or 3 *(333:)* 335
334: Style branches (or stigmas) 5 336

335 Stamens numerous *(334)* .... **Theaceae**
335: Stamens 10 or fewer .... **Linaceae**

336 Stamens 5 (sometimes with 5 staminodes as well) *(334:)* 337
336: Stamens 10 or more (staminodes if present 5 or less) 338

337 Stamens 5 usually with alternating staminodes; herbs or shrubs; leaves often with stellate hairs *(336)* .... **Sterculiaceae**
337: Stamens 5; staminodes 5; glabrous herbs; leaves entire .... **Linaceae**

338 Stamens 10, usually 3 or 4 without anthers *(336:)* .... **Geraniaceae**
338: Stamens 10 or indefinite; staminodes sometimes present; leaves often with stellate hairs .... **Sterculiaceae**

339 Stamens 1–10 *(326:)* 340
339: Stamens numerous 342

340 Stamens 5–10 *(339)* 341
340: Stamens 1–3 343

341 Stamens 5 *(340)* 344
341: Stamens 6–10 360

342 Flowers perigynous *(339:)* .... **Rosaceae**
342: Flowers hypogynous 366

343 Flowers hypogynous *(340:)* .... **Tiliaceae**
343: Flowers epigynous .... **Donatiaceae**

344 Climbers with axillary tendrils *(341)* 345
344: Non-climbers, or climbers without axillary tendrils 346

345 Corona present within corolla *(344)* .... **Passifloraceae**
345: No corona present .... **Plumbaginaceae**

346 Styles 2 or more, free *(344:)* 347
346: Style 1, with 2 or more stigmas 352

347 Stamens opposite petals *(346)* 348
347: Stamens alternating with petals 349

348 Styles 5 *(347)* .... **Plumbaginaceae**
348: Styles less than 5 .... **Rhamnaceae**

349 Leaves with conspicuous stalked glandular hairs, especially on the adaxial (upper) surface *(347:)* .... **Droseraceae**
349: Leaves without glandular hairs, or if present, inconspicuous, sessile and confined to the abaxial (lower) surface only 350

350 Leaves small, 1–2 mm long, scale-like, appressed to stem *(349:)* .... **Tamaricaceae**
350: Leaves larger than 2 mm, with a ±distinct lamina; spreading 351

351 Staminodes present; fruit a capsule *(350:)* .... **Linaceae**
351: Staminodes absent; fruit a drupe ....**Dichapetalaceae**

352 Leaves small, appressed to stem *(346:)* .... **Tamaricaceae**
352: Leaves not appressed to stem 353

353 Stamens opposite petals *(352:)* .... **Rhamnaceae**
353: Stamens alternating with petals 354

354 Herbs *(353:)* 355
354: Shrubs or trees 357

355 Stamens 5; staminodes 5 *(354)*...**Geraniaceae**
355: Stamens 5; staminodes absent 356

356 Fruit a schizocarp *(355:)*.. **Stackhousiaceae**
356: Fruit a capsule .... **Saxifragaceae**

357 Flowers perigynous or epigynous *(354:)* .... **Saxifragaceae**
357: Flowers hypogynous 358

358 Ovary 1-locular *(357:)*..**Icacinaceae**
358: Ovary 2- or more-locular 359

359 Hypogynous disc present *(358:)*..**Dichapetalaceae**
359: Hypogynous disc absent ....**Grossulariaceae**

360 Leaves peltate *(341:)* .... **Tropaeolaceae**
360: Leaves not peltate 361

361 Stamens 8, 6 of them attached to base of corolla *(360:)*.............................**Polygalaceae**
361: Stamens all hypogynous or perigynous 362

362 Stamens 7–10; if 10, some without anthers *(361:)*..................................**Geraniaceae**
362: Stamens 10, all with anthers 363

363 Style 1, with 2 or more stigmas *(362:)* 364
363: Styles several, free...365

364 Flowers hypogynous; sepals free *(363)* ....**Geraniaceae**
364: Flowers perigynous or epigynous; sepals united.................................. **Saxifragaceae**

365 Herbs *(363:)*.. **Saxifragaceae**
365: Shrubs or trees ....**Anacardiaceae**

366 Sepals imbricate *(342:)*...**Actinidiaceae**
366: Sepals valvate or united 367

367 Petals deeply incised *(366:)*..**Elaeocarpaceae**
367: Petals entire... **Tiliaceae**

368 Leaves alternate or radical *(302:)*..369
368: Leaves opposite 378

369 Styles or sessile stigmas, free *(368)* 370
369: Style 1, with 2 or more stigmas 373

370 Herbs *(369)* 371
370: Shrubs or trees 372

371 Stamens 5 *(370)* .... **Droseraceae**
371: Stamens 10 .... **Oxalidaceae**

372 Styles 2; leaflets 2, occasionally 1 *(370:)* .... **Sapindaceae**
372: Styles more than 2, or if 2 the leaflets more than 2 .... **Anacardiaceae**

373 Stamens 3; staminodes 2–5; style petaloid *(369:)* .... **Caesalpiniaceae**
373: Stamens 5 or more; style not petaloid 374

374 Stamens 5, with or without an additional 5 staminodes *(373:)* 375
374: Stamens more than 5 (if numerous, some often staminodal) 376

375 Stamens 5; staminodes absent *(374)* .... **Anacardiaceae**
375: Stamens 5, alternating with 5 usually scale-like staminodes .... **Geraniaceae**

376 Stamens 6–9; stigmas not plumose *(374:)* .... **Sapindaceae**
376: Stamens 10–numerous; stigmas plumose or not 377

377 Stamens 10; staminodes absent; stigmas plumose *(376:)* .... **Simaroubaceae**
377: Stamens numerous, some often staminodal; stigmas not plumose .... **Bombacaceae**

378 Leaves with 3 leaflets *(368:)* .... **Cunoniaceae**
378: Leaves with more than 3 leaflets 379

379 Trees *(378:)* .... **Cunoniaceae**
379: Herbs or small shrubs 380

380 Herbs; style simple with 1–5 sessile stigmas *(379:)* .... **Zygophyllaceae**
380: Herbs or small shrubs; style with 5 short stigmatic branches .... **Geraniaceae**

381 Stamens 5 *(188:)* 382
381: Stamens more than 5 394

382 Stamens opposite petals *(381)* 383
382: Stamens alternating with petals 386

383 Parasitic shrubs (mistletoes) *(382)* .... **Loranthaceae**
383: Plants not parasitic 384

384 Leaves gland-dotted *(383:)* .... **Myrtaceae**
384: Leaves not gland-dotted 385

385 Stamens attached to petals at their bases *(384:)* .... **Alangiaceae**
385: Stamens free from petals .... **Rhamnaceae**

386 Leaves gland-dotted *(382:)* .... **Myrtaceae**
386: Leaves not gland-dotted 387

387 Herbs, non-climbing, non-twining *(386:)* 388
387: Shrubs or trees, sometimes climbing or twining 389

388 Flowers in umbels or heads; styles or stigmas 2 *(387)* .... **Apiaceae**
388: Flowers not in umbels or heads; style and stigma 1 .... **Onagraceae**

389 Flowers not in umbels *(387:)* 390
389: Flowers in umbels 393

390 Leaves compound *(389)* .... **Araliaceae**
390: Leaves simple 391

391 Indumentum of simple or glandular hairs *(390:)* .... **Grossulariaceae**
391: Indumentum of stellate hairs 392

392 Flowers in subumbellate clusters *(391:)* .... **Araliaceae**
392: Flowers in elongated spikes .... **Hamamelidaceae**

393 Fruit a schizocarp, separating into 2 flattened mericarps when mature *(389:)* .... **Apiaceae**
393: Fruit a berry or drupe .... **Araliaceae**

394 Leaves gland-dotted *(381:)* 395
394: Leaves not gland-dotted 398

395 Stamens numerous *(394)* .... **Myrtaceae**
395: Stamens 10 or fewer 396

396 Stamens 10, alternating with staminodes *(395:)* .... **Myrtaceae**
396: Stamens 10 or fewer; staminodes absent 397

397 Ovary 1-locular; ovules pendulous *(396:)* .... **Combretaceae**
397: Ovary 2- or more-locular, sometimes 1-locular and then ovules axile or rarely parietal .... **Myrtaceae**

398 Leaves alternate, radical, or absent *(394:)* 399
398: Leaves opposite 407

399 Leaves compound *(398)* 400
399: Leaves simple 401

400 Stamens 2 or 3 opposite each petal *(399)* .... **Flacourtiaceae**
400: Stamens indefinite, not regularly opposite petals .... **Rosaceae**

401 Styles or stigmas more than 1 *(399:)* 402
401: Style and stigma 1 404

402 Stamens 6, attached to petals *(401)* .... **Alangiaceae**
402: Stamens 10 or more, free from petals 403

403 Stamens 10 *(402:)* .... **Anacardiaceae**
403: Stamens indefinite .... **Rosaceae**

404 Stamens indefinite *(401:)* .... **Rosaceae**
404: Stamens 10 or fewer 405

405 Herbs *(404:)* .... **Onagraceae**
405: Shrubs (sometimes climbing) or trees 406

406 Ovary 1-locular *(405:)* .... **Combretaceae**
406: Ovary 2- or more-locular .... **Grossulariaceae**

407 Leaves simple or absent *(398:)* 408
407: Leaves compound 415

408 Leaves with several conspicuous longitudinal veins *(407)* .... **Melastomataceae**
408: Midrib the only conspicuous longitudinal vein 409

409 Stamens indefinite *(408:)* .... **Punicaceae**
409: Stamens usually 10, rarely up to 13 410

410 Style 1; stigmas 1 or 2 *(409:)* 411
410: Styles 3 414

411 Leaves unequal, one of each pair much larger than other; anthers with conspicuous appendages *(410)* .... **Melastomataceae**
411: Leaves of each pair equal; anthers without appendages 412

412 Ovary 1-locular *(411:)* .... **Combretaceae**
412: Ovary 2- or more-locular 413

413 Trees of sea-shores or salt creeks *(412:)* .... **Rhizophoraceae**
413: Plants not growing in salt water .... **Saxifragaceae**

414 Petals sessile or with very short claws *(410:)* .... **Saxifragaceae**
414: Petals with slender claws .... **Malpighiaceae**

415 Leaves petiolate *(407:)* .... **Cunoniaceae**
415: Leaves sessile .... **Saxifragaceae**

416 Flowers with 1 or more long spurs *(91:)* .... **Ranunculaceae**
416: Flowers lacking spurs 417

417 Sepals 2 *(416:)* 418
417: Sepals more than 2, or whole perianth petaloid or sepaloid 419

418 Style short or absent; stigmas usually confluent *(417)* .... **Papaveraceae**
418: Styles several, free, or style 1 with several free stigmas .... **Portulacaceae**

419 Ovary superior *(417:)* 420
419: Ovary inferior 440

420 Aquatic herbs with floating or submerged leaves *(419)* .... **Nymphaeaceae**
420: Herbs (not aquatic), shrubs, or trees 421

421 Leaves alternate *(420:)* 422
421: Leaves opposite or verticillate 436

422 Climbers *(421)* 423
422: Non-climbers 425

423 Tendril climbers *(422)*..**Passifloraceae**

423: Not tendril climbers...424

  424 Branches spiny *(423:)*... **Cactaceae**

  424: Branches not spiny ....**Menispermaceae**

425 One perfect stamen (much longer than the others) and usually 4 or more imperfect stamens *(422:)*...**Anacardiaceae**

425: Perfect stamens 5 or more...426

  426 Leaves simple or absent *(425:)* 427

  426: Leaves compound...435

427 Flowers perigynous *(426)* 428

427: Flowers hypogynous..429

  428 Stamens hypogynous or inserted low in hypanthium *(427)* .... **Lythraceae**

  428: Stamens inserted on rim of hypanthium ....**Rosaceae**

429 Herbs *(427:)*...430

429: Shrubs or trees 431

  430 Ovary open at top, with sessile stigmas *(429)*.. **Resedaceae**

  430: Ovary closed; style present .... **Amaranthaceae**

431 Stamens 6–9 *(429:)* 432

431: Stamens 10 or numerous..433

  432 Plants spiny *(431)*.. **Berberidaceae**

  432: Plants without spines..**Flacourtiaceae**

433 Perianth segments 3 + 3 + 3; styles numerous *(431:)*.............................. **Magnoliaceae**

433: Sepals 5 or more; styles or stigmas 5 or fewer...434

  434 Bracteoles present, merging into sepals *(433:)* ....**Theaceae**

  434: Bracteoles absent or small ....**Flacourtiaceae**

435 Stamens 6 *(426:)* .... **Berberidaceae**

435: Stamens 10...**Mimosaceae**

  436 Leaves compound, with 3 leaflets (each pair looking like a whorl of 6 leaves) *(421:)* .... **Cunoniaceae**

  436: Leaves simple..437

437 Ovary 10–15-locular *(436:)* .... **Sonneratiaceae**

437: Ovary 3–6-locular 438

  438 Leaves with 5–7 conspicuous longitudinal veins *(437:)*..................**Melastomataceae**

  438: Midrib the only conspicuous longitudinal vein...439

439 Stamens inserted on the hypanthium; anthers opening longitudinally *(438:)* **Lythraceae**

439: Stamens at base of hypanthium; anthers opening by terminal pores .....**Melastomataceae**

  440 Aquatic herbs *(419:)*..**Nymphaeaceae**

  440: Herbs (not aquatic), shrubs, or trees...441

441 Leaves absent, their function taken over by fleshy photosynthetic stems *(440:)* .... **Cactaceae**

441: Leaves present 442

442 Leaves alternate or clustered *(441:)* 443

442: Leaves opposite 452

443 Branches spiny *(442)* 444

443: Branches without spines 445

444 Plants fleshy, leafless *(443)* .... **Cactaceae**

444: Plants woody, with leaves .... **Punicaceae**

445 Plants parasitic (mistletoes) *(443:)* .... **Loranthaceae**

445: Plants not parasitic 446

446 Leaves fleshy *(445:)* .... **Aizoaceae**

446: Leaves not fleshy 447

447 Leaves palmate *(446:)* .... **Araliaceae**

447: Leaves simple 448

448 Stamens (plus staminodes if present) indefinite *(447:)* 449

448: Stamens less than 10 450

449 Style 1; stigma 1 *(448)* .... **Punicaceae**

449: Stigmas indefinite, sessile on flat surface of ovary .... **Eupomatiaceae**

450 Stigma 1, sessile *(448:)* .... **Combretaceae**

450: Distinct style or styles present 451

451 Style 1; stigmas 2 *(450:)* .... **Alangiaceae**

451: Styles or stigmas 3–5 .... **Flacourtiaceae**

452 Leaves fleshy; stigmas 5 *(442:)* .... **Aizoaceae**

452: Leaves not fleshy; stigmas 1 or 2 453

453 Petals absent *(452:)* 454

453: Petals present 455

454 Leaves gland-dotted *(453)* .... **Myrtaceae**

454: Leaves not gland-dotted .... **Sonneratiaceae**

455 Leaves with 5–7 conspicuous longitudinal veins *(453:)* .... **Melastomataceae**

455: Midrib the only conspicuous longitudinal vein 456

456 Sepals and petals each numerous *(455:)* .... **Rhizophoraceae**

456: Sepals and petals each less than 10 457

457 Stamens 20 or more *(456:)* .... **Punicaceae**

457: Stamens less than 20 458

458 Ovary 1-locular, with c. 10 ovules *(457:)* .... **Combretaceae**

458: Ovary 2–5-locular, with 1 or 2 ovules per loculus .... **Rhizophoraceae**

459 Flowers unisexual *(11:)* 460
459: Flowers mostly bisexual 473

460 Leaves opposite *(459)* 461
460: Leaves alternate 464

461 Ovary inferior *(460)* .... **Rubiaceae**
461: Ovary superior 462

462 Gynoecium apocarpous *(461:)* .... **Monimiaceae**
462: Gynoecium syncarpous or carpel 1 463

463 Fruit a berry *(462:)* .... **Theaceae**
463: Fruit of 1–4 nutlets .... **Lamiaceae**

464 Perianth segments in 1 whorl *(460:)* 465
464: Perianth segments in 2 whorls 467

465 Ovary inferior *(464)* .... **Araliaceae**
465: Ovary superior 466

466 Stamens 6 or more in regular series around a disc-like axis; perianth shallow, cup-shaped, entire to slightly lobed *(465:)* .... **Gyrostemonaceae**
466: Stamens 1–many, not arranged as above; sepals evidently lobed .... **Euphorbiaceae**

467 Sepals 4; petals 4 *(464:)* 468
467: Sepals and petals each 5 or more 469

468 Climbers *(467)* .... **Menispermaceae**
468: Non-climbers .... **Ebenaceae**

469 Ovary superior *(467:)* 470
469: Ovary inferior 472

470 Stamens usually 10 in male flowers *(469)* .... **Ebenaceae**
470: Stamens 5 in male flowers 471

471 Fruit a capsule *(470:)* .... **Solanaceae**
471: Fruit a nut or drupe .... **Olacaceae**

472 Placentation parietal *(469:)* .... **Cucurbitaceae**
472: Placentation axile .... **Campanulaceae**

473 Ovary superior *(459:)* 474
473: Ovary inferior or half-inferior 660

474 Fertile stamens 2–4 (sometimes with additional staminodes) *(473)* 475
474: Fertile stamens 5 or more (sometimes with additional staminodes) 477

475 Stamens 3 or 4 *(474)* 476
475: Stamens 2 478

476 Stamens 3 *(475)* .... **Olacaceae**
476: Stamens 4 (sometimes with additional staminodes) 498

477 Stamens 5 *(474:)* 556
477: Stamens more than 5 642

478 Ovary divided into (usually 4) free or nearly free segments *(475:)* .... **Lamiaceae**
478: Ovary entire or slightly lobed 479

479 Flowers actinomorphic *(478:)* 480
479: Flowers zygomorphic (sometimes only slightly so) 489

480 Leaves compound *(479)* 481
480: Leaves simple or absent 482

481 Sepals 4 *(480)* .... **Oleaceae**
481: Sepals 5 .... **Verbenaceae**

482 Corolla lobes 4 *(480:)* .... **Oleaceae**
482: Corolla lobes 5 or more 483

483 Corolla lobes more than 5 *(482:)* .... **Oleaceae**
483: Corolla lobes 5 484

484 Herbs *(483:)* .... **Scrophulariaceae**
484: Shrubs, undershrubs or climbers 485

485 Climbers *(484:)* .... **Oleaceae**
485: Shrubs or undershrubs 486

486 Flowers in long terminal spikes *(485:)* .... **Verbenaceae**
486: Flowers not in spikes 487

487 Style deeply divided into 2 branches *(486:)* .... **Verbenaceae**
487: Style minutely notched at top 488

488 Corolla lobes 4 *(487:)* .... **Oleaceae**
488: Corolla lobes 5 .... **Verbenaceae**

489 Bracteoles enclosing calyx *(479:)* .... **Acanthaceae**
489: Bracteoles absent or small 490

490 Calyx divided into 2 lobes or segments *(489:)* 491
490: Calyx divided into more than 2 lobes or segments 492

491 Leaves opposite *(490)* .... **Verbenaceae**
491: Leaves, if present, alternate or radical .... **Lentibulariaceae**

492 Leaves radical or alternate *(490:)* 493
492: Leaves opposite 494

493 Ovary 1-locular; placentation parietal *(492)* .... **Gesneriaceae**
493: Ovary 2-locular; placentation axile .... **Solanaceae**

494 Leaves with viscid hairs *(492:)* 495
494: Leaves glabrous or hairs, if present, not viscid 496

495 Annual or perennial herbs *(494)* .... **Pedaliaceae**
495: Shrubs or subshrubs .... **Verbenaceae**

496 Ovary 1-locular *(494:)* .... **Gesneriaceae**
496: Ovary 2- or more-locular 497

497 Seeds flattened, 2 or 4, or up to 20 per capsule, seated on distinct hooks which persist after seed dispersal; in dried specimens (except *Acanthus*) all green parts with cystoliths (raised white streaks or dots) visible under 10× magnification *(496:)* .... **Acanthaceae**
497: Seeds not flattened, numerous, not seated on distinct hooks; cystoliths lacking .... **Scrophulariaceae**

498 Ovary apocarpous *(476:)* .... **Monimiaceae**
498: Ovary syncarpous or carpel 1 499

499 Flowers actinomorphic or nearly so *(498:)* 500
499: Flowers zygomorphic 533

500 Leaves opposite, verticillate or radical *(499)* 501
500: Leaves alternate or absent in mature plants 503

501 Leaves radical *(500)* 502
501: Leaves opposite or verticillate 516

502 Sepals 4, free; petals 4, united *(501)* .... **Plantaginaceae**
502: Sepals 5, free; petals 5, united .... **Acanthaceae**

503 Leaves alternate, bipinnate *(500:)* .... **Mimosaceae**
503: Leaves alternate or absent in mature plant, not bipinnate 504

504 Corolla lobes 3 *(503:)* .... **Polygalaceae**
504: Corolla lobes 4 or 5 505

505 Corolla lobes 4 *(504:)* 506
505: Corolla lobes 5 511

506 Stamens alternating with corolla lobes *(505)* 507
506: Stamens opposite corolla lobes 510

507 Prostrate or erect plants, not twining *(506)* 508
507: Twining plants 509

508 Prostrate annuals *(507)* .... **Boraginaceae**
508: Erect perennials .... **Solanaceae**

509 Leaves absent *(507:)* .... **Cuscutaceae**
509: Leaves present .... **Cardiopteridaceae**

510 Ovary 1-locular with several ovules *(506:)* .... **Myrsinaceae**
510: Ovary 2-locular with 1 ovule per loculus .... **Sapotaceae**

511 Leaves absent *(505:)* .... **Cuscutaceae**
511: Leaves present 512

512 Leaves with viscid hairs *(511:)* 513
512: Leaves glabrous or hairs, if present, not viscid 514

513 Seeds endospermic *(512)* .... **Solanaceae**
513: Seeds non-endospermic .... **Pedaliaceae**

514 Anthers connivent around the style *(512:)* .... **Solanaceae**
514: Anthers not connivent 515

515 Fruit a drupe *(514:)* .... **Myoporaceae**
515: Fruit a capsule or berry .... **Solanaceae**

516 Ovary divided into (usually 4) separate segments *(501:)* 517
516: Ovary entire or lobed 518

517 Style terminal *(516)* .... **Verbenaceae**
517: Style gynobasic, rarely terminal .... **Lamiaceae**

518 Sepals 4 *(516:)* 519
518: Sepals 5 or more, or calyx 2-lipped or truncate 526

519 Ovary 1-locular, with 2 parietal placentas *(518)* .... **Gentianaceae**
519: Ovary 2- or 4-locular 520

520 Ovary 4-locular *(519:)* .... **Verbenaceae**
520: Ovary 2-locular 521

521 Shrubs or trees *(520:)* 522
521: Herbs 523

522 Staminode present in addition to fertile stamens (flowers bisexual) *(521)* .... **Verbenaceae**
522: Staminodes absent (except in female flowers of dioecious species) .... **Loganiaceae**

523 Leaves in whorls, usually of 3 *(521:)* .... **Scrophulariaceae**
523: Leaves opposite 524

524 Ovary half-inferior *(523:)* .... **Rubiaceae**
524: Ovary quite superior 525

525 Capsule circumscissile *(524:)* .... **Plantaginaceae**
525: Capsule septicidal .... **Loganiaceae**

526 Corolla 4-lobed *(518:)* .... **Verbenaceae**
526: Corolla 5-lobed 527

527 Leaves compound *(526:)* 528
527: Leaves simple or absent 529

528 Seeds winged *(527)* .... **Bignoniaceae**
528: Seeds unwinged .... **Verbenaceae**

529 Bracteoles large, ±enclosing calyx *(527:)* .... **Acanthaceae**
529: Bracteoles absent or not enclosing calyx 530

530 Placentas parietal *(529:)* .... **Gesneriaceae**
530: Placentas axile 531

531 Ovary 4-locular, with 1 ovule per loculus *(530:)* .... **Verbenaceae**
531: Ovary 2-locular 532

532 Herbs or small shrubs; ovary with several ovules per loculus *(531:)* .... **Scrophulariaceae**
532: Trees; ovary with numerous ovules per loculus .... **Bignoniaceae**

533 Leaves varying in type on one plant *(499:)* 534
533: Leaves all of one type, either simple, compound or reduced to scales 536

534 Leaves mostly in whorls of 3 *(533)* .... **Bignoniaceae**
534: Leaves opposite, the upper ones sometimes becoming alternate 535

535 Upper leaves simple, lower leaves compound; ovary 2- or 4-locular with 1–many ovules per loculus *(534:)* .... **Pedaliaceae**
535: Leaves very variable, simple or with 3–5 leaflets; ovary 2-locular with 2 ovules per loculus .... **Verbenaceae**

536 Leaves all simple or reduced to scales *(533:)* 537
536: Leaves all compound 554

537 Leaves reduced to scales; plants without chlorophyll *(536)* .... **Orobanchaceae**
537: Leaves not reduced to scales; plants green 538

538 Leaves all radical or all alternate *(537:)* 539
538: Leaves at least in part opposite or verticillate 545

539 Leaves radical *(538)* .... **Scrophulariaceae**
539: Leaves all alternate 540

540 Calyx of 3 outer and 2 inner sepals, all free; petals 3, united *(539:)* .... **Polygalaceae**
540: Calyx of 5 free or united sepals in 1 whorl; petals 5, united 541

541 Ovary 4-locular *(540:)* .... **Myoporaceae**
541: Ovary 2-locular 542

542 Herbs (sometimes climbing) *(541:)* 543
542: Shrubs or small trees 544

543 Corolla actinomorphic or nearly so, usually spreading *(542)* .... **Solanaceae**
543: Corolla 2-lipped .... **Scrophulariaceae**

544 Stigmas 2; fruit a capsule or berry *(542:)* .... **Solanaceae**
544: Stigma 1; fruit a drupe .... **Myoporaceae**

545 Lower leaves opposite; upper leaves alternate *(538:)* 546
545: Leaves all opposite or verticillate 547

546 Ovary 2-locular *(545)* .... **Scrophulariaceae**
546: Ovary 4-locular .... **Pedaliaceae**

547 Ovary divided into 4 nearly separate segments at maturity *(545:)*.................. **Lamiaceae**
547: Ovary simple or lobed 548

548 Ovary 4- or 8-locular *(547:)* 549
548: Ovary 1- or 2-locular..550

549 Ovary 4-locular with 1 ovule per loculus *(548)* .... **Verbenaceae**
549: Ovary 8-locular with 1 ovule per loculus ....**Pedaliaceae**

550 Ovary 1-locular; ovules numerous *(548:)*... **Gesneriaceae**
550: Ovary 2-locular; ovules 1–numerous...551

551 Seeds seated on distinct hooks which ......persist after seed dispersal; in dried specimens (except *Acanthus*) all green parts with cystoliths .... (raised white streaks or dots) visible under 10× magnification *(550:)* .... **Acanthaceae**
551: Seeds not seated on hooks; cystoliths absent..552

552 Ovules 1 or 2 per loculus; undershrubs, shrubs or woody vines, rarely trees *(551:)* .... **Verbenaceae**
552: Ovules 2 or more per loculus; herbs, shrubs or trees 553

553 Herbs or small shrubs; ovules 2 or more per loculus; seeds winged or unwinged *(552:)* ....**Scrophulariaceae**
553: Small or large trees; ovules numerous; seeds with papery wings............... **Bignoniaceae**

554 Climbers, usually woody *(536:)*.. **Bignoniaceae**
554: Shrubs or trees 555

555 Fifth stamen represented by a staminode; seeds with papery wings *(554:)* **Bignoniaceae**
555: Fifth stamen absent; seeds unwinged .... **Verbenaceae**

556 Latex present *(477)*...557
556: Latex absent 565

557 Leaves opposite, verticillate or absent *(556)* 558
557: Leaves alternate...560

558 Leaves absent *(557)*... **Asclepiadaceae**
558: Leaves opposite or verticillate 559

559 Stamens lacking a coronal appendage; pollen grains single *(558:)*.............**Apocynaceae**
559: Stamens mostly with a coronal appendage; pollen grains cohering in tetrads or pollinia .... **Asclepiadaceae**

560 Twiners *(557:)*..561
560: Non-twiners...562

561 Fruits winged *(560)* ....**Cardiopteridaceae**
561: Fruits not winged .... **Convolvulaceae**

562 Flowers zygomorphic *(560:)*.. **Campanulaceae**
562: Flowers actinomorphic 563

563 Anthers connivent around or above stigma *(562:)* ....**Apocynaceae**
563: Anthers free...564

564 Stamens alternating with lobes or angles of corolla *(563:)* .... **Convolvulaceae**
564: Stamens opposite corolla lobes ....**Sapotaceae**

565 Leafless parasites *(556:)* ....**Cuscutaceae**
565: Leafy plants..566

566 Gynoecium apocarpous or divided into 2 or more free segments *(565:)* 567
566: Gynoecium syncarpous, the ovary entire or lobed, or carpel 1 572

567 Leaves opposite, verticillate or absent *(566)* 568
567: Leaves alternate or radical 570

568 Leaves absent *(567)* .... **Asclepiadaceae**
568: Leaves opposite or verticillate 569

569 Perianth segments (calyx plus corolla) 10 or fewer *(568:)* ....**Apocynaceae**
569: Perianth segments c. 15 .... **Monimiaceae**

570 Inflorescence a monochasial cyme, uncoiling as the flowers open *(567:)*.....................
....**Boraginaceae**
570: Inflorescence not as above 571

571 Plants slender, creeping perennials, rooting at nodes *(570:)* .... **Convolvulaceae**
571: Plants ±erect...**Boraginaceae**

572 Leaves alternate, in alternate pairs, or clustered *(566:)*...573
572: Leaves verticillate or opposite 575

573 Leaves compound *(572)*..574
573: Leaves simple..595

574 Leaves stipulate *(573)*..**Mimosaceae**
574: Leaves exstipulate ....**Leeaceae**

575 Leaves verticillate *(572:)* 576
575: Leaves opposite..577

576 Shrubs or trees *(575)* ....**Apocynaceae**
576: Floating herbs ....**Droseraceae**

577 Flowers actinomorphic *(575:)*..578
577: Flowers zygomorphic 593

578 Leaves compound *(577)*.. **Bignoniaceae**
578: Leaves simple..579

579 Style 1 with 5–many branches, or styles 5 *(578:)* 580
579: Style 1 with 1–4 stigmas or branches 581

580 Styles or style branches 5 *(579)* ....**Plumbaginaceae**
580: Style 1, apex divided into many minute stigmatic branches .... **Nyctaginaceae**

581 Style 1 with 3 or 4 branches *(579:)*..582
581: Style 1 with 1 or 2 stigmas..583

582 Style with 4 branches *(581)* .... **Polemoniaceae**

582: Style with 3 branches.. 592

583 Inflorescence a monochasial cyme *(581:)*.. **Boraginaceae**

583: Inflorescence not a monochasial cyme 584

584 Anthers cohering about style *(583:)* 585

584: Anthers quite free 587

585 Herbs *(584)* .... **Caryophyllaceae**

585: Shrubs.. 586

586 Leaves opposite *(585:)* .... **Apocynaceae**

586: Leaves alternate.. **Solanaceae**

587 Stamens alternating with corolla lobes *(584:)* 588

587: Stamens opposite corolla lobes .... **Primulaceae**

588 Ovary l-locular *(587)*.. 589

588: Ovary 2- or 4-locular 590

589 Stipules small, scarious *(588)* .... **Caryophyllaceae**

589: Stipules absent .... **Gentianaceae**

590 Plants (including the inflorescence) densely covered with cottony or woolly hairs *(588:)*... **Verbenaceae**

590: Not as above... 591

591 Leaves all opposite, usually stipulate *(590)*.. **Loganiaceae**

591: Leaves on non-flowering parts alternate, exstipulate .... **Solanaceae**

592 Stamens free from corolla *(582:)* .... **Frankeniaceae**

592: Stamens epipetalous .... **Polemoniaceae**

593 Leaves compound *(577:)* .... **Bignoniaceae**

593: Leaves simple... 594

594 Ovary 4- or occasionally 2-locular *(593:)* .... **Verbenaceae**

594: Ovary l-locular; leaves with viscid hairs .... **Pedaliaceae**

595 Petals 3 *(573:)*.. **Polygalaceae**

595: Petals 4 or 5 596

596 Style with indusium (pollen cup surrounding stigma) *(595:)* 597

596: No indusium present.. 598

597 Corolla actinomorphic or nearly so *(596)*.. **Brunoniaceae**

597: Corolla zygomorphic, usually split down one side................................ **Goodeniaceae**

598 Flowers zygomorphic *(596:)*.. 599

598: Flowers actinomorphic 600

599 Flowers only slightly zygomorphic; seeds numerous in a berry or capsule *(598)*... **Solanaceae**

599: Flowers distinctly zygomorphic; seeds 1 or 2 in 2 or 4 distinct nutlets ...... **Boraginaceae**

600 Stamens completely free from petals *(598:)* ... 601
600: Stamens attached to petals, sometimes only slightly so at base ... 610

601 Stigmas 3–5 *(600)* ... 602
601: Stigmas 1 or 2 ... 603

602 Ovary 3–5-locular; fruit of 3–5 nutlets *(601)* ... **Stackhousiaceae**
602: Ovary of 5 carpels but unilocular; fruit a single nut ... **Plumbaginaceae**

603 Stamens opposite corolla lobes *(601:)* ... 604
603: Stamens alternating with corolla lobes ... 606

604 Nectar-secreting disc conspicuous, embedding base of ovary *(603)* ... **Olacaceae**
604: Nectar-secreting disc absent ... 605

605 Ovary 1-locular with several ovules *(604:)* ... **Myrsinaceae**
605: Ovary 2- or more-locular with 1 ovule per loculus ... **Sapotaceae**

606 Herbs *(603:)* ... 607
606: Trees, shrubs, climbers, or twiners ... 608

607 Leaves with glandular hairs; corolla segments only united in short ring at the base *(606)* ... **Byblidaceae**
607: Leaves not as above; corolla segments cohering to form a tube, but free at the base ... **Stackhousiaceae**

608 Calyx covered at base with usually numerous imbricate sepaloid bracteoles *(606:)* ... **Epacridaceae**
608: Bracteoles absent, or not covering base of calyx ... 609

609 Anthers versatile; ovules 1 or 2 in ovary *(608:)* ... **Olacaceae**
609: Anthers not versatile; ovules more than 2 in ovary ... **Pittosporaceae**

610 Stamens almost free from but usually detached with petals *(600:)* ... **Pittosporaceae**
610: Stamens distinctly epipetalous, though sometimes attached near the base of corolla tube ... 611

611 Inflorescence a monochasial cyme *(610:)* ... 612
611: Inflorescence not a monochasial cyme ... 614

612 Styles 2, free *(611)* ... **Hydrophyllaceae**
612: Style 1, with 1 or more stigmas ... 613

613 Fruit a capsule or berry *(612:)* ... **Solanaceae**
613: Fruit a drupe or divided into nutlets ... **Boraginaceae**

614 Style 1 *(611:)* ... 615
614: Styles 2–5 ... 619

615 Stigmas 3–8 *(614)* ... 616
615: Stigmas 1 or 2, or stigma sessile ... 620

616 Stigmas 5–8 *(615)* ... 617
616: Stigmas 3 or 4 ... 618

617 Stigmas 5 *(616)* .... **Plumbaginaceae**
617: Stigmas 6–8 .... **Convolvulaceae**

618 Stigmas 3 *(616:)* .... **Polemoniaceae**
618: Stigmas 4 639

619 Styles 5, free *(614:)* .... **Plumbaginaceae**
619: Styles 2, free 640

620 Stamens opposite corolla lobes *(615:)* 621
620: Stamens alternating with corolla lobes 623

621 Herbs *(620)* .... **Primulaceae**
621: Shrubs or trees 622

622 Ovary l-locular, with central placenta *(621:)* .... **Myrsinaceae**
622: Ovary 2- or more-locular .... **Sapotaceae**

623 Leaves simple or absent from mature plant *(620:)* 624
623: Leaves compound 637

624 Herbs, growing in marshes or in water *(623)* .... **Menyanthaceae**
624: Herbs (not aquatic), shrubs or trees, sometimes climbers 625

625 Base of calyx ±covered by imbricate bracts and bracteoles; bracteoles sometimes only 2 *(624:)* .... **Epacridaceae**
625: Bracteoles absent, or not covering base of calyx 626

626 Climbers, twiners, or prostrate plants *(625:)* 627
626: Plants ±erect 628

627 Anthers connivent in cone around style, dehiscing by pores or slits; ovary 2-locular, usually with many ovules *(626)* .... **Solanaceae**
627: Anthers not connivent; ovary 1- or 2-locular; ovules 2 or 4 per loculus **Convolvulaceae**

628 Herbs (sometimes coarse), usually annual *(626:)* 629
628: Shrubs or small trees 630

629 Ovules 2 or more per loculus *(628)* .... **Solanaceae**
629: Ovules 1 per loculus .... **Boraginaceae**

630 Ovary 1–3-locular *(628:)* 631
630: Ovary 4- or 5-locular 635

631 Ovary l-locular *(630)* .... **Monimiaceae**
631: Ovary 2- or 3-locular 632

632 Ovary 3-locular *(631:)* .... **Solanaceae**
632: Ovary 2-locular 633

633 Ovules 1 or 2 per locule *(632:)* 634
633: Ovules more than 2 per loculus .... **Solanaceae**

634 Ovules 1 per loculus *(633)* .... **Myoporaceae**
634: Ovules 2 per loculus .... **Boraginaceae**

635 Ovary usually 5-locular *(630:)*.......... **Epacridaceae**
635: Ovary 4-locular 636

636 Fruit a drupe or nut; ovules 1 per loculus *(635:)* .... **Boraginaceae**
636: Fruit a berry or capsule; ovules usually more than 1 per loculus.......... **Solanaceae**

637 Tendril climbers *(623:)*.......... **Polemoniaceae**
637: Not tendril climbers but sometimes twiners.......... 638

638 Leaves palmate *(637:)* .... **Convolvulaceae**
638: Leaves pinnate.......... **Solanaceae**

639 Usually annuals, with slender creeping or trailing stems; ovary 2-locular *(618:)*.......... **Convolvulaceae**
639: Tall shrubs or trees; ovary 4-locular.......... **Boraginaceae**

640 Each of the 2 styles divided into 2 branches *(619:)* .... **Convolvulaceae**
640: Each style simple.......... 641

641 Ovary 2-locular, with numerous ovules *(640:)* .... **Hydrophyllaceae**
641: Ovary 2-locular, with 2 ovules per loculus.......... **Convolvulaceae**

642 Latex present *(477:)* .... **Sapotaceae**
642: Latex absent 643

643 Leaves pinnatisect or compound *(642:)*.......... 644
643: Leaves simple or reduced to phyllodes.......... 648

644 Leaves pinnatisect *(643)* .... **Ranunculaceae**
644: Leaves compound 645

645 Leaves bipinnate *(644:)* .... **Mimosaceae**
645: Leaves pinnate or 3-foliolate 646

646 Gynoecium apocarpous *(645:)* .... **Crassulaceae**
646: Gynoecium syncarpous or carpel 1.......... 647

647 Style 1; ovary 1-locular *(646:)* .... **Mimosaceae**
647: Styles 3–5; ovary 3–5-locular .... **Oxalidaceae**

648 Gynoecium apocarpous *(643:)* 649
648: Gynoecium syncarpous or carpel 1.......... 650

649 Style 1 *(648)* .... **Rutaceae**
649: Styles as many as carpels.......... **Crassulaceae**

650 Perfect stamens alternating with staminodes (sometimes scale-like) *(648:)*.......... **Sapotaceae**
650: Stamens all perfect 651

651 Stamens 10 or fewer *(650:)*.......... 652
651: Stamens indefinite.......... 656

652 Style 1, the apex divided into many minute stigmatic branches *(651)* **Nyctaginaceae**
652: Styles or stigmas 5 or fewer, apex not as above.......... 653

653 Stamens united *(652:)* ... **Polygalaceae**
653: Stamens free ... 654

654 Stamens free from corolla, hypogynous *(653:)* ... **Ericaceae**
654: Stamens epipetalous ... 655

655 Style and stigma 1 *(654:)* ... **Solanaceae**
655: Styles or stigmas 2 or more ... **Ebenaceae**

656 Ovary of 1 carpel, 1-locular; style and stigma 1 *(651:)* ... **Mimosaceae**
656: Ovary syncarpous, mostly 3–5-locular; styles or stigmas 2 or more ... 657

657 Pedicel with a pair of bracts *(656:)* ... **Theaceae**
657: Pedicel lacking bracts ... **Actinidiaceae**

658 Leaves opposite or verticillate *(473:)* ... 659
658: Leaves alternate, radical, or absent ... 675

659 Petals 4 *(658)* ... 660
659: Petals 5 or more ... 663

660 Leaves compound *(659)* ... **Caprifoliaceae**
660: Leaves simple ... 661

661 Stamens epipetalous *(660:)* ... **Rubiaceae**
661: Stamens free from petals ... 662

662 Ovary l-locular *(661:)* ... **Grossulariaceae**
662: Ovary 2–5-locular ... **Campanulaceae**

663 Petals 5 *(659:)* ... 664
663: Petals more than 5 ... 673

664 Stamen 1 *(663)* ... **Valerianaceae**
664: Stamens 4 or 5 ... 665

665 Stamens 4 *(664:)* ... 666
665: Stamens 5 ... 668

666 Flowers in heads surrounded by involucre of bracts *(665)* ... **Dipsacaceae**
666: Flowers not in heads ... 667

667 Herbs *(666:)* ... **Gesneriaceae**
667: Shrubs ... **Caprifoliaceae**

668 Plants parasitic (mistletoes) *(665:)* ... **Loranthaceae**
668: Plants not parasitic ... 669

669 Stamens free from petals *(668:)* ... 670
669: Stamens epipetalous ... 671

670 Style expanded into an indusium *(669)* ... **Goodeniaceae**
670: Style without indusium ... **Campanulaceae**

671 Flowers zygomorphic *(669:)* .... **Caprifoliaceae**
671: Flowers actinomorphic 672

672 Leaves stipulate *(671:)* .... **Rubiaceae**
672: Leaves exstipulate .... **Caprifoliaceae**

673 Styles or stigmas 3 or 5 *(663:)* .... **Rubiaceae**
673: Style 1; stigmas 1 or 2 674

674 Plants parasitic (mistletoes) *(673:)* .... **Loranthaceae**
674: Plants not parasitic .... **Rubiaceae**

675 Plants parasitic (mistletoes) *(658:)* .... **Loranthaceae**
675: Plants not parasitic 676

676 Stamens 2–4 *(675:)* 677
676: Stamens 5 or more 679

677 Stamens 2; gynandrous *(676)* .... **Stylidiaceae**
677: Stamens 3 or 4 678

678 Stamens 3 *(677:)* .... **Cucurbitaceae**
678: Stamens 4 .... **Campanulaceae**

679 Stamens 5 *(676:)* 680
679: Stamens more than 5 689

680 Style expanded into an indusium *(679)* .... **Goodeniaceae**
680: Style without indusium 681

681 Flowers zygomorphic, corolla tube usually split down one side *(680:)* **Campanulaceae**
681: Flowers actinomorphic 682

682 Prostrate plants or climbers; tendrils large *(681:)* .... **Cucurbitaceae**
682: Non-climbers; tendrils absent 683

683 Stamens alternating with corolla lobes *(682:)* 684
683: Stamens opposite corolla lobes 687

684 Ovary l-locular *(683)* .... **Menyanthaceae**
684: Ovary 2- or more-locular 685

685 Stems ±succulent, hollow; flowers in dense spikes *(684:)* .... **Sphenocleaceae**
685: Stems not succulent, solid; flowers racemose or axillary 686

686 Fruit a capsule *(685:)* .... **Campanulaceae**
686: Fruit a berry .... **Epacridaceae**

687 Herbs *(683:)* .... **Primulaceae**
687: Trees or climbers 688

688 Trees or climbers; stigma 1 *(687:)* .... **Myrsinaceae**
688: Trees; stigmas 3 .... **Alangiaceae**

689 Stamens 6 *(679:)* ..... **Alangiaceae**
689: Stamens 10 or more 690

690 Stamens 10 *(689:)* ..... **Ericaceae**
690: Stamens numerous 691

691 Leaves, if present, caducous *(690:)* ..... **Cactaceae**
691: Leaves persistent 692

692 Leaves gland-dotted *(691:)* ..... **Myrtaceae**
692: Leaves not gland-dotted ..... **Symplocaceae**

693 Flowers unisexual *(10:)* 694
693: Flowers mostly bisexual 777

694 Leafless stem parasite embedded in host; only the flowers emergent *(693)* ..... **Rafflesiaceae**
694: Not an embedded parasite (though sometimes leafless) 695

695 Leaves or scales in whorls of 3 or more *(694:)* 696
695: Leaves or scales alternate, opposite, or absent 698

696 Shrubs or trees *(695)* ..... **Casuarinaceae**
696: Aquatic herbs 697

697 Ovary inferior *(696:)* ..... **Haloragaceae**
697: Ovary superior ..... **Ceratophyllaceae**

698 Latex present *(695:)* 699
698: Latex absent 701

699 Separate male and female flowers inside pear-shaped receptacle which opens by narrow aperture at top *(698)* ..... **Moraceae**
699: Not as above 700

700 Leaves stipulate; ovary 1-locular with 1 ovule *(699:)* ..... **Moraceae**
700: Leaves exstipulate; ovary 2- or more-locular ..... **Euphorbiaceae**

701 Perianth segments 2 or 3 *(698:)* 702
701: Perianth segments 4 or more, or perianth obscurely lobed or truncate 717

702 Perianth segments 2 *(701)* 703
702: Perianth segments 3 708

703 Ovary superior *(702)* 704
703: Ovary inferior 707

704 Climbers *(703)* ..... **Menispermaceae**
704: Non-climbers 705

705 Ovary 2- or 3-locular; styles 2 or 3 *(704:)* ..... **Euphorbiaceae**
705: Ovary l-locular; styles 2 706

706 Leaves stipulate *(705:)* ..... **Urticaceae**
706: Leaves exstipulate ..... **Chenopodiaceae**

707 Flowers minute, in heads, surrounded by an involucre of bracts; style 1 with bifid stigma *(703:)* .... **Asteraceae**

707: Flowers not in heads, or if in heads, lacking an involucre of bracts; styles 2 (± fused at base) .... **Gunneraceae**

708 Ovary inferior *(702:)* 709

708: Ovary superior 710

709 Herbs *(708)* .... **Gunneraceae**

709: Parasitic shrubs (mistletoes) .... **Viscaceae**

710 Succulent root parasites without chlorophyll, 5–10 cm high with scale-like leaves *(708:)* .... **Balanophoraceae**

710: Herbs, shrubs, or trees, not parasitic 711

711 Style or stigma 1 *(710:)* 712

711: Styles or style branches 2 or more 715

712 Stigma penicillate *(711)* .... **Urticaceae**

712: Stigma not penicillate 713

713 Leaves compound *(712:)* .... **Sapindaceae**

713: Leaves simple 714

714 Leaves with 7–20 primary veins on each side of midrib *(713:)* .... **Myristicaceae**

714: Midrib the only prominent vein, if any .... **Santalaceae**

715 Ovary 2- or 3-locular *(711:)* .... **Euphorbiaceae**

715: Ovary l-locular, with 1 ovule 716

716 Leaves stipulate *(715:)* .... **Polygonaceae**

716: Leaves exstipulate .... **Amaranthaceae**

717 Perianth segments 4 *(701:)* 718

717: Perianth segments 5 or more, or perianth obscurely lobed or truncate 742

718 Plants parasitic on roots or stems *(717)* 719

718: Plants not parasitic 720

719 Leafless succulents, parasitic on roots *(718)* .... **Balanophoraceae**

719: Shrubs parasitic on stems (mistletoes) .... **Viscaceae**

720 Ovary or gynoecium superior *(718:)* 721

720: Ovary inferior 740

721 Gynoecium apocarpous *(720)* 722

721: Gynoecium syncarpous or carpel 1 725

722 Styles 4, connate *(721)* .... **Sterculiaceae**

722: Styles free 723

723 Leaves alternate *(722:)* .... **Phytolaccaceae**

723: Leaves opposite 724

724 Leaves simple *(723:)* .... **Monimiaceae**
724: Leaves compound .... **Ranunculaceae**

725 Leaf terminating in a tendril or pitcher provided with a lid *(721:)* .... **Nepenthaceae**
725: Leaf not terminating in a tendril or pitcher, or leaves absent 726

726 Styles or stigmas penicillate *(725:)* .... **Urticaceae**
726: Neither styles nor stigmas penicillate 727

727 Styles 1 or 2 *(726:)* 728
727: Styles 3–6 729

728 Styles 2 *(727)* .... **Ulmaceae**
728: Style 1 730

729 Placentation axile *(727:)* .... **Euphorbiaceae**
729: Placentation parietal .... **Flacourtiaceae**

730 Leaves simple or absent *(728:)* 731
730: Leaves compound 739

731 Leaves alternate *(730)* 732
731: Leaves opposite .... **Urticaceae**

732 Leaves without stinging hairs, or leaves absent *(731)* 733
732: Leaves with stinging hairs .... **Urticaceae**

733 Stamens 2–4 in male flowers *(732)* 734
733: Stamens 6 or more in male flowers 737

734 Stamens 2 in male flowers *(733)* .... **Thymelaeaceae**
734: Stamens usually 4 in male flowers 735

735 Leaves not expanded at time of flowering; stigma sessile *(734:)* .... **Santalaceae**
735: Leaves present at time of flowering 736

736 Leaves stipulate *(735:)* .... **Urticaceae**
736: Leaves exstipulate .... **Phytolaccaceae**

737 Stamens 6 in male flowers *(733:)* .... **Lauraceae**
737: Stamens 10 or numerous in male flowers 738

738 Ovary glabrous *(737:)* .... **Flacourtiaceae**
738: Ovary with hooked bristles .... **Phytolaccaceae**

739 Leaves stipulate *(730:)* .... **Rosaceae**
739: Leaves exstipulate .... **Sapindaceae**

740 Herbs *(720:)* .... **Haloragaceae**
740: Shrubs or trees 741

741 Fruit a nut *(740:)* .... **Fagaceae**
741: Fruit a capsule .... **Datiscaceae**

742 Ovary or gynoecium superior *(717:)* 743
742: Ovary inferior 772

743 Gynoecium apocarpous *(742)* 744
743: Gynoecium syncarpous or carpel 1 748

744 Leaves opposite *(743)* .... **Monimiaceae**
744: Leaves alternate 745

745 Perianth segments 6 *(744:)* .... **Menispermaceae**
745: Perianth segments 5 746

746 Leaves gland-dotted *(745:)* .... **Rutaceae**
746: Leaves not gland-dotted 747

747 Ovules 1 per carpel *(746:)* .... **Phytolaccaceae**
747: Ovules 2 or more per carpel .... **Sterculiaceae**

748 Leaves alternate, radical, or absent *(743:)* 749
748: Leaves opposite 769

749 Climbers *(748)* 750
749: Non-climbers 752

750 Styles 3, free *(749)* .... **Amaranthaceae**
750: Styles connate or united; stigmas 3 751

751 Stamens 2–5 in male flowers; plants monoecious *(750:)* .... **Euphorbiaceae**
751: Stamens c. 8 in male flowers; plants usually dioecious .... **Polygonaceae**

752 Perianth segments 5, or perianth obscurely lobed or truncate *(749:)* 753
752: Perianth segments 6 766

753 Leaves simple or absent *(752)* 754
753: Leaves compound 764

754 Perianth shallow cup-shaped, scarcely lobed; stamens ±sessile *(753)* .... **Gyrostemonaceae**
754: Perianth ±erect, clearly lobed; stamens with filaments 755

755 Styles or stigmas 8 or more *(754:)* .... **Phytolaccaceae**
755: Styles or stigmas 1–3 (if style 2 or 3, stigmas sometimes 4 or 6, i.e. style bifid) 756

756 Style and stigma 1 *(755:)* 757
756: Styles or stigmas usually 2 or 3 759

757 Ovary 3- or more-locular *(756)* .... **Sapindaceae**
757: Ovary 1-locular 758

758 Style terminal; ovule 1 *(757:)* .... **Euphorbiaceae**
758: Style gynobasic; ovules 2 .... **Surianaceae**

759 Herbs *(756:)* 760
759: Shrubs or trees 761

760 Ovary l-locular *(759)* .... **Amaranthaceae**
760: Ovary 2- or more-locular .... **Euphorbiaceae**

761 Ovary 2- or 3-locular *(759:)* .... **Euphorbiaceae**
761: Ovary l-locular with 1 ovule 762

762 Leaf base sheathing *(761:)* .... **Polygonaceae**
762: Leaf base not sheathing 763

763 Leaves stipulate *(762:)* .... **Ulmaceae**
763: Leaves exstipulate .... **Chenopodiaceae**

764 Herbs *(753:)* .... **Rosaceae**
764: Shrubs or trees 765

765 Leaves 3-foliolate *(764:)* .... **Euphorbiaceae**
765: Leaves pinnate .... **Sapindaceae**

766 Slender creeping perennials *(752:)* .... **Polygonaceae**
766: Shrubs or trees 767

767 Perianth in 2 whorls each of 3 united segments *(766:)* .... **Ebenaceae**
767: Perianth segments usually all free 768

768 Perianth segments in 1 series; style 1, entire or shortly lobed *(767:)*........ **Sapindaceae**
768: Perianth segments usually in 2 series; styles usually 3, simple or divided .... **Euphorbiaceae**

769 Styles 2 or more *(748:)* .... **Euphorbiaceae**
769: Style 1, with 1 or 2 stigmas 770

770 Woody climbers *(769:)* .... **Nyctaginaceae**
770: Shrubs or trees 771

771 Stamens 2 in male flowers *(770:)* .... **Oleaceae**
771: Stamens more than 2 .... **Sapindaceae**

772 Leaves compound *(742:)* .... **Apiaceae**
772: Leaves simple 773

773 Style and stigma 1, or stigma sessile *(772:)* .... **Combretaceae**
773: Styles and stigmas 2–8 774

774 Styles or stigmas 2 *(773:)* 775
774: Styles or stigmas 3–8 776

775 Fruit indehiscent, 1-seeded (a cypsela) *(774)* .... **Asteraceae**
775: Fruit 2-locular, breaking at maturity into 2 unicarpellate units (a schizocarp)... **Apiaceae**

776 Fruit a nut *(774:)* .... **Fagaceae**
776: Fruit a capsule .... **Datiscaceae**

777 Latex present *(693:)* 778
777: Latex absent 782

778 Ovary inferior *(777)* 779
778: Ovary superior 781

779 Perianth small, insignificant or absent *(778)* .... **Moraceae**
779: Perianth ±showy, petaloid 780

780 Perianth strongly zygomorphic *(779:)* .... **Asteraceae**
780: Perianth ±actinomorphic .... **Rubiaceae**

781 Flowers unisexual; ovary 3-locular *(778:)* .... **Euphorbiaceae**
781: Flowers bisexual; ovary 2–many-locular .... **Papaveraceae**

782 Ovary or gynoecium superior *(777:)* 783
782: Ovary inferior 951

783 Gynoecium apocarpous *(782)* 784
783: Gynoecium syncarpous or carpel 1 802

784 Perianth segments 2 or 4 *(783)* 785
784: Perianth segments 5 or 6 791

785 Perianth segments 2 *(784)* .... **Winteraceae**
785: Perianth segments 4 786

786 Climbers *(785:)* .... **Ranunculaceae**
786: Non-climbers 787

787 Herbs *(786:)* 788
787: Shrubs or trees 789

788 Leaves radical *(787)* .... **Ranunculaceae**
788: Leaves alternate .... **Phytolaccaceae**

789 Perianth segments united *(787:)* .... **Sterculiaceae**
789: Perianth segments free 790

790 Leaves stipulate *(789:)* .... **Magnoliaceae**
790: Leaves exstipulate .... **Monimiaceae**

791 Perianth segments 5 *(784:)* 792
791: Perianth segments 6 795

792 Leaves gland-dotted *(791)* .... **Rutaceae**
792: Leaves, if present, not gland-dotted 793

793 Leaves opposite *(792:)* .... **Cunoniaceae**
793: Leaves alternate, radical or absent 794

794 Leaves all alternate, or absent *(793:)* .... **Phytolaccaceae**
794: Leaves radical, or radical and alternate .... **Ranunculaceae**

795 Leaves opposite *(791:)* .... **Monimiaceae**
795: Leaves alternate or radical 796

796 Leaves mostly radical *(795:)*....797
796: Leaves all alternate....798

797 Leaf pitchers present *(796)*....**Cephalotaceae**
797: Leaf pitchers absent....**Ranunculaceae**

798 Aquatic herbs with peltate leaves *(796:)*....**Cabombaceae**
798: Shrubs, trees or woody climbers....799

799 Woody climbers *(798:)*....**Menispermaceae**
799: Shrubs or trees, non-climbers....800

800 Stamens 8 *(799:)*....**Phytolaccaceae**
800: Stamens indefinite....801

801 Leaves distichous; receptacle short *(800:)*....**Annonaceae**
801: Leaves not distichous; receptacle elongated....**Magnoliaceae**

802 Perianth segments 1–3 *(783:)*....803
802: Perianth segments 4–6....812

803 Perianth segment 1 *(802)*....**Caryophyllaceae**
803: Perianth segments 2 or 3....804

804 Perianth segments 2 *(803:)*....805
804: Perianth segments 3....807

805 Stamens 5 or fewer *(804)*....**Chenopodiaceae**
805: Stamens numerous....806

806 Herbs or small shrubs *(805:)*....**Papaveraceae**
806: Trees....**Winteraceae**

807 Leaves alternate or absent *(804:)*....808
807: Leaves opposite or verticillate....811

808 Leaves absent *(807)*....**Chenopodiaceae**
808: Leaves alternate....809

809 Styles 2 or 3 *(808:)*....**Amaranthaceae**
809: Style 1....810

810 Tendrils present *(809:)*....**Vitaceae**
810: Tendrils absent....**Caryophyllaceae**

811 Stigma 1 *(807:)*....**Lythraceae**
811: Stigmas 3....**Elatinaceae**

812 Perianth segments 5 or 6 *(802:)*....813
812: Perianth segments 4....814

813 Perianth segments 5 *(812)*....869
813: Perianth segments 6....928

814 Leaves alternate, radical, or absent *(812:)* 815
814: Leaves opposite or verticillate 854

815 Style and stigma 1 *(814)* 816
815: Styles or stigmas more than 1 846

816 Stamens (excluding staminodes) 2 or 3 *(815)* 817
816: Stamens 4 or more 819

817 Stamens 3 (with or without additional staminodes) *(816)* 818
817: Stamens 2 823

818 Stamens 3; staminodes absent *(817)* .... **Rosaceae**
818: Stamens 3; staminode 1 .... **Proteaceae**

819 Stamens 4 or 5 *(816:)* 820
819: Stamens 6 or more 821

820 Stamens 4 *(819)* 827
820: Stamens 5 .... **Rosaceae**

821 Stamens 6 *(819:)* 822
821: Stamens more than 6 840

822 Fruit a berry *(821)* .... **Lauraceae**
822: Fruit an achene .... **Rosaceae**

823 Leaves simple or absent *(817:)* 824
823: Leaves compound 826

824 Leaves radical or absent *(823)* .... **Lentibulariaceae**
824: Leaves alternate 825

825 Herbs; perianth segments free *(824:)* .... **Brassicaceae**
825: Shrubs; perianth segments united .... **Thymelaeaceae**

826 Floating aquatics *(823:)* .... **Lentibulariaceae**
826: Rooted land plants .... **Rosaceae**

827 Plants usually climbers with leaf-opposed tendrils *(820)* .... **Vitaceae**
827: Plants without tendrils 828

828 Leaves compound *(827:)* 829
828: Leaves simple 831

829 Stamens adnate to perianth segments *(828)* .... **Proteaceae**
829: Stamens not adnate to perianth segments 830

830 Fruit an achene *(829:)* .... **Rosaceae**
830: Fruit a legume .... **Caesalpiniaceae**

831 Leaves with stinging hairs *(828:)* .... **Urticaceae**
831: Leaves without stinging hairs 832

832 Stamens distinctly adnate to perianth segments *(831:)* 833
832: Stamens adhering to base of perianth, or free from it 834

833 Stamens same number as and opposite perianth segments and often sessile on them *(832)* .... **Proteaceae**
833: Stamens same number as and alternate with perianth segments, or twice as many, on short filaments .... **Elaeagnaceae**

834 Flowers in axillary spikes *(832:)* 835
834: Flowers not in spikes 837

835 Leaves glabrous or with scattered hairs *(834)* 836
835: Underside of leaves white with close-set hairs .... **Urticaceae**

836 Perianth segments united into 4-lobed floral tube *(835)* .... **Opiliaceae**
836: Perianth segments not united .... **Santalaceae**

837 Perianth petaloid *(834:)* 838
837: Perianth sepaloid 839

838 Stamens same number as and opposite perianth segments *(837)* .... **Proteaceae**
838: Stamens same number as and alternate with perianth segments or more numerous .... **Phytolaccaceae**

839 Flowers ebracteate, in terminal racemes *(837:)* .... **Brassicaceae**
839: Flowers bracteate, in clusters, cymes, or heads .... **Urticaceae**

840 Leaves simple *(821:)* 841
840: Leaves compound 845

841 Herbs *(840)* 842
841: Shrubs or trees 843

842 Sepals 2, valvate, completely enclosing bud; ovules several in each loculus *(841)* .... **Papaveraceae**
842: Sepals not as above; ovule 1 in each loculus .... **Phytolaccaceae**

843 Stamens 10 or fewer *(841:)* .... **Thymelaeaceae**
843: Stamens indefinite 844

844 Leaves gland-dotted *(843:)* .... **Winteraceae**
844: Leaves not gland-dotted .... **Tiliaceae**

845 Shrubs or trees *(840:)* .... **Caesalpiniaceae**
845: Herbs .... **Rosaceae**

846 Stamens 4 or fewer *(815:)* 847
846: Stamens 5 or more 850

847 Herbs, either aquatic or growing in wet places; leaves radical, floating or absent; sepals 2; petals united; corolla 2-lipped *(846)* .... **Lentibulariaceae**
847: Plants not as above 848

848 Leaves with ochrea *(847:)* .... **Polygonaceae**
848: Leaves without ochrea 849

849 Herbs or shrubs; leaves covered with mealy scales *(848:)* .... **Chenopodiaceae**
849: Trees .... **Ulmaceae**

850 Stamens 5–10 *(846:)*.. 851
850: Stamens numerous.. 853

851 Style 1; stigmas usually 2 *(850)* .... **Sapindaceae**
851: Styles more than 1 852

852 Trees with irritant hairs; stipules reniform; fruit a large drupe *(851:)* **Davidsoniaceae**
852: Herbs without irritant hairs; stipules sheath-like; fruit a small nut......... **Polygonaceae**

853 Ovary 3- to 5-locular *(850:)*.................................. **Nymphaeaceae**
853: Ovary 1-locular .... **Papaveraceae**

854 Style and stigma 1 *(814:)*.. 855
854: Styles or stigmas more than 1 864

855 Stamens 2, 3 or 5 *(854)*.. 856
855: Stamens 4 or 8... 859

856 Stamens 3 or 5 *(855)* .... **Lythraceae**
856: Stamens 2.. 857

857 Stamens free from perianth, united into a cup at base *(856:)* .... **Amaranthaceae**
857: Stamens adnate to perianth 858

858 Annual herbs, frequently in moist situations *(857:)*.......................... **Lythraceae**
858: Small shrubs.. **Thymelaeaceae**

859 Stamens 8 *(855:)* .... **Thymelaeaceae**
859: Stamens 4.. 860

860 Leaves with stinging hairs *(859:)*.................................. **Urticaceae**
860: Leaves without stinging hairs...................................... 861

861 Stamens distinctly adnate to perianth *(860:)* 862
861: Stamens free from perianth or attached at the base of the perianth segments............. 863

862 Shrubs or trees *(861)* .... **Proteaceae**
862: Herbs .... **Lythraceae**

863 Herbs *(861:)*.. **Amaranthaceae**
863: Shrubs or trees .... **Santalaceae**

864 Stamen 1 *(854:)*... **Caryophyllaceae**
864: Stamens 4 or more.. 865

865 Stamens 4 *(864:)* 866
865: Stamens more than 4... 867

866 Stamens alternating with the perianth lobes *(865)* .... **Aizoaceae**
866: Stamens opposite the perianth lobes.......................... **Santalaceae**

867 Styles 2 *(865:)* .... **Cunoniaceae**
867: Styles 4 868

868 Stamens indefinite *(867:)* .... **Aizoaceae**
868: Stamens 8 .... **Cunoniaceae**

869 Leaves alternate, radical, or absent *(813)* 870
869: Leaves opposite or verticillate 913

870 Stamens 5 or fewer *(869)* 871
870: Stamens more than 5 892

871 Style and stigma 1 *(870)* 872
871: Styles or stigmas more than 1 880

872 Climbers with leaf-opposed tendrils *(871)* .... **Vitaceae**
872: Non-climbers, or climbers without leaf-opposed tendrils 873

873 Leaves compound *(872:)* .... **Caesalpiniaceae**
873: Leaves simple or absent 874

874 Flowers in clusters of 2–4, surrounded by conspicuous coloured bracts *(873:)* .... **Nyctaginaceae**
874: Flowers not as above 875

875 Stamens 3 or fewer, with or without staminodes *(874:)* 876
875: Stamens 5, all with anthers 877

876 Stamens 2 or 3, with or without anthers, united at base into a short cup *(875)* .... **Amaranthaceae**
876: Stamens 3; staminodes 5 .... **Olacaceae**

877 Herbs or undershrubs *(875:)* .... **Amaranthaceae**
877: Shrubs or trees 878

878 Stamens opposite perianth segments *(877:)* .... **Santalaceae**
878: Stamens alternate with perianth segments 879

879 Ovary surrounded by nectar-secreting disc *(878:)* .... **Rhamnaceae**
879: Ovary not surrounded by nectar-secreting disc .... **Sterculiaceae**

880 Twiners or climbers *(871:)* 881
880: Not climbers or twiners 884

881 Tendril climbers *(880)* 882
881: Twiners, without tendrils 883

882 Tendrils axillary *(881)* .... **Passifloraceae**
882: Tendrils terminating inflorescence .... **Polygonaceae**

883 Perianth segments free; styles 3 *(881:)* .... **Amaranthaceae**
883: Perianth segments united; style 1, with 2 short stigmas .... **Rhamnaceae**

884 Herbs *(880:)* 885
884: Shrubs or trees 889

885 Ovary 3–5-locular, with several ovules in each loculus *(884)* 886
885: Ovary 1-locular, with 1–several ovules 887

886 Flowers hypogynous; calyx free, divided to base or nearly so *(885)* .... **Molluginaceae**
886: Flowers perigynous; calyx entirely or partly adnate to ovary, or free but with a distinct tube .... **Aizoaceae**

887 Leaves with ochrea *(885:)* .... **Polygonaceae**
887: Leaves without ochrea 888

888 Flowers with 1 bract and usually 1 or 2 bracteoles *(887:)* .... **Amaranthaceae**
888: Flowers without bracts or bracteoles .... **Chenopodiaceae**

889 Stamens opposite perianth segments *(884:)* 890
889: Stamens alternating with perianth segments 891

890 Perianth segments free; tall shrubs or trees *(889)* .... **Ulmaceae**
890: Perianth segments united; shrubs, usually small .... **Chenopodiaceae**

891 Stamens 5; staminodes 5; ovary 5-locular *(889:)* .... **Sterculiaceae**
891: Stamens 5; ovary 2- or 3-locular .... **Rhamnaceae**

892 Leaves simple or absent *(870:)* 893
892: Leaves compound 910

893 Style 1 *(892)* 894
893: Styles 2 or more, free 905

894 Stigma large, peltate *(893)* .... **Surianaceae**
894: Stigma not peltate 895

895 Flowers in clusters of 3–5, surrounded by 3 large coloured bracteoles *(894:)* .... **Nyctaginaceae**
895: Flowers not surrounded by conspicuous bracteoles 896

896 Climbers, shrubs or trees *(895:)* 897
896: Herbs, non-climbers 898

897 Climbers *(896)* .... **Polygonaceae**
897: Shrubs or trees 900

898 Stamens indefinite *(896:)* .... **Molluginaceae**
898: Stamens 10 or fewer 899

899 Flowers hypogynous *(898:)* .... **Polygonaceae**
899: Flowers perigynous .... **Aizoaceae**

900 Perianth segments united *(897:)* 901
900: Perianth segments free 903

901 Leaves absent; stems flat and green *(900)* .... **Polygonaceae**
901: Leaves present 902

902 Stamens 10 or fewer; stigmas 2 or 3 *(901:)* .... **Sapindaceae**
902: Stamens indefinite; stigma 1 .... **Elaeocarpaceae**

903 Flowers small, in heads or spikes; stamens exserted *(900:)* ..... **Mimosaceae**
903: Flowers not in heads or spikes; stamens usually not exserted 904

904 Seeds endospermic; stipules present, often caducous *(903:)* ..... **Flacourtiaceae**
904: Seeds non-endospermic; stipules absent ..... **Lauraceae**

905 Styles 2 or 3 *(893:)* 906
905: Styles 5 or more 907

906 Styles 2 *(905)* ..... **Polygonaceae**
906: Styles 3 908

907 Styles 5 *(905:)* ..... **Aizoaceae**
907: Styles c. 8 ..... **Phytolaccaceae**

908 Ovary 1-locular; ovule 1 *(906:)* ..... **Polygonaceae**
908: Ovary 3-locular; ovules several per loculus 909

909 Flowers hypogynous; calyx free, divided to base or nearly so *(908:)* ..... **Molluginaceae**
909: Flowers perigynous; calyx entirely or partly adnate to ovary, or free but with a distinct tube ..... **Aizoaceae**

910 Leaves bipinnate *(892:)* ..... **Mimosaceae**
910: Leaves pinnate 911

911 Stigmas 2 *(910:)* ..... **Sapindaceae**
911: Stigma 1 912

912 Ovary 1-locular *(911:)* ..... **Caesalpiniaceae**
912: Ovary 2- or more-locular ..... **Sapindaceae**

913 Style and stigma 1 *(869:)* 914
913: Styles or style-branches more than 1 919

914 Leaves gland-dotted *(913)* ..... **Myrtaceae**
914: Leaves not gland-dotted 915

915 Stamens free from perianth *(914:)* 916
915: Stamens adnate to perianth 917

916 Perianth segments free *(915)* ..... **Amaranthaceae**
916: Perianth segments united ..... **Nyctaginaceae**

917 Opposite leaves unequal in size *(915:)* ..... **Aizoaceae**
917: Opposite leaves equal in size 918

918 Stamens 10 *(917:)* ..... **Thymelaeaceae**
918: Stamens less than 10 ..... **Lythraceae**

919 Stamen 1 *(913:)* ..... **Caryophyllaceae**
919: Stamens 2 or more 920

920 Stamens 2–5 *(919:)* 921
920: Stamens more than 5 925

921 Stamens adnate to perianth *(920)* .... **Aizoaceae**
921: Stamens free from perianth 922

922 Ovules more than 1 *(921:)* 923
922: Ovule 1 924

923 Placentation free-central *(922)* .... **Caryophyllaceae**
923: Placentation axile .... **Molluginaceae**

924 Perianth segments scarious *(922:)* .... **Amaranthaceae**
924: Perianth segments herbaceous .... **Chenopodiaceae**

925 Flowers perigynous; stamens borne on calyx tube *(920:)* .... **Aizoaceae**
925: Flowers hypogynous 926

926 Shrubs or trees *(925:)* .... **Cunoniaceae**
926: Herbs 927

927 Ovary 1-locular; leaves opposite or verticillate *(926:)* .... **Caryophyllaceae**
927: Ovary 3–5-locular; leaves alternate, often clustered in axils so as to appear verticillate .... **Aizoaceae**

928 Leaves alternate, radical, or absent *(813:)* 929
928: Leaves opposite or verticillate 945

929 Sepals 2, often caducous; petals 4 *(928)* 930
929: Perianth in 1 series, or if in 2 series usually of 3 + 3 segments 931

930 Flowers actinomorphic; stamens numerous *(929)* .... **Papaveraceae**
930: Flowers zygomorphic; stamens 6 .... **Fumariaceae**

931 Stamens 5 or more *(929:)* 932
931: Stamens 3 933

932 Stamens 5 or 6, sometimes with staminodes *(931)* 935
932: Stamens more than 6 939

933 Climbers with leaf-opposed tendrils *(931:)* .... **Vitaceae**
933: Trees or shrubs 934

934 Style and stigma 1 *(933:)* .... **Lauraceae**
934: Styles 2 or 3 .... **Euphorbiaceae**

935 Climbers with leaf-opposed tendrils *(932)* .... **Vitaceae**
935: Plants without tendrils 936

936 Leaves large, compound *(935:)* .... **Burseraceae**
936: Leaves simple 937

937 Perianth segments united *(936:)* .... **Ebenaceae**
937: Perianth segments free 938

938 Leaves with ochrea *(937:)* .... **Polygonaceae**
938: Leaves without ochrea .... **Euphorbiaceae**

939 Leafless parasitic twiners *(932:)* ....**Lauraceae**
939: Non-twiners 940

940 Style and stigma 1 *(939:)*..941
940: Styles or stigmas 2 or 3..944

941 Flowers with 1 or more long spurs *(940)*... **Ranunculaceae**
941: Flowers lacking spurs..942

942 Ovary 1-locular *(941:)*..**Lauraceae**
942: Ovary 2- or more-locular 943

943 Leaves gland-dotted *(942:)* ....**Rutaceae**
943: Leaves not gland-dotted...**Elaeocarpaceae**

944 Perianth segments free *(940:)* ....**Polygonaceae**
944: Perianth segments united ....**Ebenaceae**

945 Stamens 3 *(928:)* ....**Elatinaceae**
945: Stamens 9 or more..946

946 Stamens 9, usually with 3 staminodes *(945:)*...**Lauraceae**
946: Stamens 10 or indefinite 947

947 Woody climbers *(946:)* .... **Monimiaceae**
947: Non-climbers...948

948 Leaves trifoliolate *(947:)* .... **Cunoniaceae**
948: Leaves not trifoliolate...949

949 Herbs *(948:)*.. **Lythraceae**
949: Shrubs or small trees 950

950 Carpels 2 *(949:)* ....**Aquifoliaceae**
950: Carpels 4–15 .... **Sonneratiaceae**

951 Plants parasitic (mistletoes) *(782:)*...**Loranthaceae**
951: Plants not parasitic 952

952 Leaves alternate, radical, or absent *(951:)*...953
952: Leaves opposite or verticillate 973

953 Leaves gland-dotted *(952)* 954
953: Leaves not gland-dotted, or leaves absent 955

954 Stamens 10 *(953)*...**Combretaceae**
954: Stamens indefinite .... **Myrtaceae**

955 Perianth actinomorphic *(953:)* 956
955: Perianth zygomorphic...971

956 Perianth quite entire, or of 3 segments *(955)*.................................. **Aristolochiaceae**
956: Perianth of 4–6 segments..957

957 Perianth segments 4 *(956:)* 958
957: Perianth segments 5 or 6 963

958 Stamens 2 or 4 *(957)* 959
958: Stamens 5 or more 960

959 Stamens 2 *(958)* .... **Gunneraceae**
959: Stamens 4 961

960 Stamens 5 *(958:)* .... **Asteraceae**
960: Stamens 6 or more .... **Aizoaceae**

961 Flowers not in umbels or heads *(959:)* .... **Santalaceae**
961: Flowers in umbels or heads 962

962 Flowers in umbels *(961:)* .... **Araliaceae**
962: Flowers in heads surrounded by involucral bracts .... **Asteraceae**

963 Stamens 5 *(957:)* 964
963: Stamens more than 5 969

964 Anthers united around style *(963)* .... **Asteraceae**
964: Anthers free 965

965 Herbs *(964:)* .... **Apiaceae**
965: Shrubs or trees 966

966 Styles 2, free *(965:)* .... **Araliaceae**
966: Style 1, with 1 or 2 stigmas 967

967 Stamens opposite perianth segments *(966:)* .... **Santalaceae**
967: Stamens alternating with perianth segments 968

968 Leaves simple and entire *(967:)* .... **Rhamnaceae**
968: Leaves compound or dissected .... **Araliaceae**

969 Leaves compound *(963:)* .... **Araliaceae**
969: Leaves simple 970

970 Trees; stamens usually 10 *(969:)* .... **Combretaceae**
970: Herbs or shrubs; stamens usually indefinite .... **Aizoaceae**

971 Fruit a cypsella *(955:)* .... **Asteraceae**
971: Fruit a nut, a many-seeded capsule, or fleshy and indehiscent 972

972 Stigmas 1 or 2, each with indusium (pollen cup surrounding stigma) *(971:)* .... **Goodeniaceae**
972: Stigmas 3–6, without indusium .... **Aristolochiaceae**

973 Leaves gland-dotted *(952:)* .... **Myrtaceae**
973: Leaves not gland-dotted 974

974 Perianth segments 3 or 4 *(973:)* 975
974: Perianth segments 5 or 6 984

975 Perianth segments 3 *(974)*.......... **Rubiaceae**
975: Perianth segments 4.......... 976

976 Stamens 2–5 *(975:)*.......... 977
976: Stamens 8 or more.......... 978

977 Stamens 2 *(976)*.......... **Thymelaeaceae**
977: Stamens 4 or 5.......... 980

978 Stamens 8 *(976:)*.......... **Cunoniaceae**
978: Stamens numerous.......... 979

979 Leaves simple *(978:)*.......... **Myrtaceae**
979: Leaves compound or unifoliolate.......... **Flacourtiaceae**

980 Stamens 4 or 5; anthers fused together (syngenesious) *(977:)*.......... **Asteraceae**
980: Stamens 4; anthers not syngenesious.......... 981

981 Aquatic herbs *(980:)*.......... **Haloragaceae**
981: Plants not aquatic.......... 982

982 Leaves in whorls of 4–8 *(981:)*.......... **Rubiaceae**
982: Leaves opposite.......... 983

983 Stamens alternating with perianth segments *(982:)*.......... **Rubiaceae**
983: Stamens opposite perianth segments.......... **Santalaceae**

984 Perianth segments 5 *(974:)*.......... 985
984: Perianth segments 6.......... 989

985 Stamen 1 *(984)*.......... **Valerianaceae**
985: Stamens 5 or more.......... 986

986 Stamens indefinite *(985:)*.......... **Aizoaceae**
986: Stamens 5.......... 987

987 Anthers syngenesious *(986:)*.......... **Asteraceae**
987: Anthers free.......... 988

988 Anthers opposite perianth segments *(987:)*.......... **Santalaceae**
988: Anthers alternating with perianth segments.......... **Rubiaceae**

989 Leaves compound *(984:)*.......... **Caprifoliaceae**
989: Leaves simple.......... 990

990 Stamens 3 *(989:)*.......... **Rubiaceae**
990: Stamens 10 or more.......... 991

991 Stamens 10 *(990:)*.......... **Portulacaceae**
991: Stamens numerous.......... **Sonneratiaceae**

992 Latex present *(2:)*.......... 993
992: Latex absent.......... 994

993 Styles or stigmas 3 or more *(992)* ....**Euphorbiaceae**

993: Style or stigma 1..**Moraceae**

994 Succulent herbs 5–10 cm high, parasitic on roots; leaves absent or scale-like *(992:)* ... .**Balanophoraceae**

994: Plants not parasitic; leaves green if present 995

995 Flowers mostly unisexual *(994:)* 996

995: Flowers mostly bisexual 1008

996 Climbers or twiners *(995)* 997

996: Non-climbers...998

997 Placentation apical *(996)* .... **Cannabaceae**

997: Placentation basal..**Piperaceae**

998 Leaves alternate *(996:)* 999

998: Leaves opposite 1000

999 Leaves in whorls of 4 or more, or reduced to scales *(998)* 1001

999: Leaves not as above 1002

1000 Aquatic herbs, usually non-littoral; seeds endospermic *(998:)*.......... **Callitrichaceae**

1000: Littoral shrubs; seeds non-endospermic .... **Bataceae**

1001 Shrubs or trees; leaves reduced to minute scales *(999)* .... **Casuarinaceae**

1001: Aquatic herbs; leaves entire or divided but not reduced to scales............**Haloragaceae**

1002 Plants monoecious *(999:)* 1003

1002: Plants dioecious 1005

1003 Herbs or undershrubs; flowers in heads *(1002)* ....**Asteraceae**

1003: Trees; flowers otherwise 1004

1004 Leaves serrate-crenate; deciduous *(1003:)*.. **Betulaceae**

1004: Leaves entire; evergreen ....**Euphorbiaceae**

1005 Leaves palmately dissected *(1002:)*.. **Cannabaceae**

1005: Leaves not dissected 1006

1006 Both male and female flowers in dense spikes *(1005:)* .... **Salicaceae**

1006: Female flowers solitary or racemose; male flowers solitary or in spikes............1007

1007 Male flowers in catkins; female flowers with involucre of bracts but no perianth *(1006:)* ....**Balanopaceae**

1007: Male flowers solitary or in open spikes; perianth shallow cup-shaped, inconspicuous ... . **Gyrostemonaceae**

1008 Herbaceous plants, growing only on rocks in running water *(995:)*... **Podostemaceae**

1008: Land plants..1009

1009 Stamens 10 or fewer, usually 2 or 3 *(1008:)*...**Piperaceae**

1009: Stamens indefinite ....**Mimosaceae**

Monocotyledons

1010 Plants of marine or brackish habitats *(1:)* 1011
1010: Plants of fresh-water or land habitats 1017

1011 Leaves ligulate *(1010)* 1012
1011: Leaves eligulate 1014

1012 Plants of brackish habitats *(1011)* .... **Zannichelliaceae**
1012: Marine plants 1013

1013 Leaf blade and sheath shed leaving a circular scar *(1012:)* .... **Cymodoceaceae**
1013: Leaf blade shed but sheath persistent and fibrous .... **Posidoniaceae**

1014 Leaves with 7 or more longitudinal veins *(1011:)* .... **Hydrocharitaceae**
1014: Leaves with 1–5 longitudinal veins 1015

1015 Leaves 1–3 per shoot *(1014:)* .... **Hydrocharitaceae**
1015: Leaves 4 or more per shoot 1016

1016 Carpel solitary; stigmas 2, filiform *(1015:)* .... **Zosteraceae**
1016: Carpels 4–8; stigma 1, peltate .... **Ruppiaceae**

1017 Floating plants with 1 or more flat, leaf-like stems 1–8 mm in diameter, cohering by their edges, with or without roots hanging from the undersurface *(1010:)* **Lemnaceae**
1017: Plants not as above 1018

1018 Flowers unisexual *(1017:)* 1019
1018: Flowers bisexual 1042

1019 Leaves opposite or verticillate *(1018)* 1020
1019: Leaves alternate, radical, crowded at apex of stem, or absent 1022

1020 Slender, twining land plants *(1019)* .... **Dioscoreaceae**
1020: Aquatic or marsh plants 1021

1021 Perianth in male flowers absent or of one segment *(1020:)* .... **Najadaceae**
1021: Perianth segments in male flowers 3 + 3; stamens 3–9 .... **Hydrocharitaceae**

1022 Leaves simple *(1019:)* 1023
1022: Leaves compound 1041

1023 Flowers closely packed in a dense, simple, unbranched spadix, with a usually convolute, coloured, or petal-like spathe arising from base *(1022)* .... **Araceae**
1023: Spathe sometimes present, but inflorescence not as above and often branched 1024

1024 Trees or shrubs, rarely climbers; aerial stem woody *(1023:)* 1025
1024: Herbs (sometimes large, e.g. banana) 1026

1025 Perianth absent; trees, shrubs, or climbers *(1024)* .... **Pandanaceae**
1025: Perianth segments 3 + 3; climbers .... **Smilacaceae**

1026 Flowers inconspicuous, often minute, within imbricate bracts or scales, in heads or spikelets; perianth absent or of 1–8 scales or bristles, usually concealed within bracts *(1024:)* 1027

1026: Flowers otherwise 1031

1027 Flowers small in spherical androgynous heads 2–8 mm in diameter without conspicuous bracts; mostly marsh or aquatic plants *(1026)* .... **Eriocaulaceae**

1027: Flowers in spikelets surrounded by glume-like bracts 1028

1028 Leaf-sheath with connate margins *(1027:)* .... **Cyperaceae**

1028: Leaf-sheath with free margins, sometimes overlapping 1029

1029 Leaves ligulate *(1028:)* .... **Poaceae**

1029: Leaves eligulate 1030

1030 Wiry plants with jointed stems *(1029:)* .... **Restionaceae**

1030: Tiny, slender plants without erect stems .... **Hydatellaceae**

1031 Aquatic or marsh plants *(1026:)* 1032

1031: Land plants 1035

1032 Ovary inferior *(1031)* .... **Hydrocharitaceae**

1032: Ovary superior 1033

1033 Plants dioecious *(1032:)* .... **Hanguanaceae**

1033: Plants monoecious 1034

1034 Flowers in cylindrical, terminal spikes *(1033:)* .... **Typhaceae**

1034: Flowers in globular, lateral heads .... **Sparganiaceae**

1035 Climbers *(1031:)* 1036

1035: Non-climbers 1037

1036 Ovary superior; stems often spiny *(1035)* .... **Smilacaceae**

1036: Ovary inferior; stems not spiny at least in upper part .... **Dioscoreaceae**

1037 Ovary inferior *(1035:)* .... **Musaceae**

1037: Ovary superior 1038

1038 Leaves large, pinnately or palmately divided (palms) *(1037:)* .... **Arecaceae**

1038: Leaves otherwise 1039

1039 Leaves with a well-defined petiole; lamina with many cross-nerves; fruit a fleshy, thick-walled, 1–3-seeded drupe *(1038:)* .... **Hanguanaceae**

1039: Leaves without a well-defined petiole; lamina parallel-veined; fruit a berry, capsule or dry and indehiscent 1040

1040 Fruit containing many small dust-like seeds; perianth segments sepaloid; fruit a capsule *(1039:)* .... **Juncaceae**

1040: Fruit containing 3 large seeds, or if more than 3, then not dust-like; perianth segments petaloid; fruit a berry, capsule or dry and indehiscent .... **Liliaceae**

1041 Ovary superior *(1022:)* .... **Arecaceae**

1041: Ovary inferior .... **Dioscoreaceae**

1042 Flowers closely packed in a simple spadix, usually with coloured spathe ±enclosing it *(1018:)* .... **Araceae**

1042: Flowers not in spadix; inflorescence often branched; spathe sometimes present 1043

1043 Gynoecium apocarpous *(1042:)* 1044

1043: Gynoecium syncarpous or carpel 1 1051

1044 Land plants *(1043)* 1045

1044: Aquatic or marsh plants 1047

1045 Woody plants; leaves compound, or pinnately or palmately divided (palms) *(1044)* .... **Arecaceae**

1045: Small herbaceous plants; leaves, if present, entire 1046

1046 Saprophyte, lacking chlorophyll; leaves reduced to scales *(1045:)* .... **Triuridaceae**

1046: Tufted chlorophyllous herbs; leaves linear .... **Centrolepidaceae**

1047 Perianth segments 2; stamens 6; carpels 3 *(1044:)* .... **Aponogetonaceae**

1047: Perianth segments 3 or more 1048

1048 Perianth segments 4; stamens 4; carpels 4 *(1047:)* .... **Potamogetonaceae**

1048: Perianth segments 3–6, rarely 4; stamens 3–numerous; carpels 3–numerous 1049

1049 Perianth segments all similar in texture and colour *(1048:)* .... **Juncaginaceae**

1049: The two perianth whorls different in texture and/or colour 1050

1050 Gynoecium of 3 or more free carpels; fruits achenes *(1049:)* .... **Alismataceae**

1050: Gynoecium of c. 6 free carpels; fruits follicles .... **Limnocharitaceae**

1051 Ovary superior or perianth absent *(1043:)* 1052

1051: Ovary inferior 1084

1052 Flowers inconspicuous, often minute, within imbricate bracts or scales (glumes), in spikelets; perianth absent or of 1–8 scales or bristles, usually concealed within bracts *(1051)* 1053

1052: Flowers otherwise 1057

1053 Leaves ligulate *(1052)* 1054

1053: Leaves eligulate 1055

1054 Embryo visible through fruit wall *(1053)* .... **Poaceae**

1054: Embryo not visible through fruit wall .... **Cyperaceae**

1055 Stamens more than 1 *(1053:)* .... **Cyperaceae**

1055: Stamen 1 1056

1056 Small annuals; inflorescence simple *(1055:)* .... **Centrolepidaceae**

1056: Rhizomatous perennials; inflorescence usually branched .... **Cyperaceae**

1057 Perianth segments 4 or fewer *(1052:)* 1058

1057: Perianth segments 6 (rarely 5) 1061

1058 Stamen 1 *(1057)* .... **Philydraceae**

1058: Stamens 3 or 4 1059

1059 Stamens 3 *(1058:)* .... **Xyridaceae**
1059: Stamens 4 1060

1060 Leaves alternate; twiners *(1059:)* .... **Stemonaceae**
1060: Leaves radical; inflorescence spicate .... **Araceae**

1061 Leaves compound (palms) *(1057:)* .... **Arecaceae**
1061: Leaves simple or absent 1062

1062 Stems woody; leaves broad (palms) *(1061:)* .... **Arecaceae**
1062: Not as above 1063

1063 Stamens 3 (rarely 2) *(1062:)* 1064
1063: Stamens 6 (rarely 5) 1069

1064 Inner perianth segments united *(1063)* .... **Xyridaceae**
1064: Inner perianth segments free 1065

1065 The two perianth whorls different in texture and/or colour *(1064:)* .... **Commelinaceae**
1065: Perianth segments all similar in texture and colour 1066

1066 Stamens inserted at base of inner perianth segments *(1065:)* .... **Haemodoraceae**
1066: Stamens free from perianth 1067

1067 Perianth segments petaloid *(1066:)* .... **Liliaceae**
1067: Perianth segments sepaloid 1068

1068 Carpels free or almost free; stigmas sessile *(1067:)* .... **Juncaginaceae**
1068: Carpels fused; style 1, stigmas 3 .... **Juncaceae**

1069 Leaf tips prolonged into tendrils *(1063:)* 1070
1069: Not as above 1071

1070 Corolla c. 3 mm long *(1069)* .... **Flagellariaceae**
1070: Corolla c. 10 mm long .... **Liliaceae**

1071 The two perianth whorls different in texture and/or colour *(1069:)* 1072
1071: Perianth segments all similar in texture and colour 1075

1072 Much-branched leafy climbers *(1071)* .... **Smilacaceae**
1072: Rosette or scrambling plants 1073

1073 Inflorescence spicate; glandular hairs present *(1072:)* .... **Commelinaceae**
1073: Flowers solitary or inflorescence cymose; if spicate no glandular hairs 1074

1074 Inner perianth segments fringed *(1073:)* .... **Liliaceae**
1074: Inner perianth segments not fringed .... **Commelinaceae**

1075 Perianth segments petaloid *(1071:)* 1076
1075: Perianth segments sepaloid 1080

1076 Aquatic plants, floating or rooted *(1075)* .... **Pontederiaceae**
1076: Land plants 1077

1077 Coarse woody climbers; venation predominantly reticulate *(1076:)* .... **Smilacaceae**
1077: Non-climbers or, if climbers, the venation convergent 1078

1078 Inflorescence a tall woody spike *(1077:)* .... **Xanthorrhoeaceae**
1078: Inflorescence otherwise 1079

1079 Much-branched leafy climbers *(1078:)* .... **Smilacaceae**
1079: Not as above .... **Liliaceae**

1080 Marsh or aquatic plants *(1075:)* .... **Juncaginaceae**
1080: Land plants 1081

1081 Climbers *(1080:)* .... **Araceae**
1081: Non-climbers 1082

1082 Style branched; stigmas 3 *(1081:)* .... **Juncaceae**
1082: Style 1, simple 1083

1083 Inflorescence a tall woody spike *(1082:)* .... **Xanthorrhoeaceae**
1083: Inflorescence otherwise .... **Liliaceae**

1084 Flowers gynandrous (i.e. with stamens adnate to pistil) *(1051:)* 1085
1084: Flowers not gynandrous 1087

1085 Flowers strongly gynandrous *(1084)* .... **Orchidaceae**
1085: Flowers only weakly gynandrous 1086

1086 Venation pinnate *(1085:)* .... **Cannaceae**
1086: Venation convergent .... **Orchidaceae**

1087 Submerged aquatics; leaf lamina submerged or floating; styles or stigmas 6, each 2-lobed *(1084:)* .... **Hydrocharitaceae**
1087: Not as above 1088

1088 Leaf lamina deeply dissected *(1087:)* .... **Taccaceae**
1088: Leaves entire or with serrate margins 1089

1089 Climbing plants; leaves alternate with many longitudinal veins from midrib; veinlets reticulate *(1088:)* .... **Smilacaceae**
1089: Not as above 1090

1090 Venation obviously pinnate *(1089:)* 1091
1090: Venation convergent (middle vein sometimes stronger than others) parallel, or obscured by the thickness of leaf 1095

1091 Stamens 5 *(1090)* .... **Musaceae**
1091: Stamens 1–3 1092

1092 Ligule present at junction of leaf-sheath and lamina *(1091:)* 1093
1092: Leaves eligulate 1094

1093 Leaves 2-ranked *(1092)* .... **Zingiberaceae**
1093: Leaves more than 2-ranked .... **Costaceae**

1094 Pulvinus present at junction of petiole (or leaf-sheath) and blade *(1092:)* .... **Marantaceae**

1094: Pulvinus absent .... **Cannaceae**

1095 Stamens 3 *(1090:)* 1096

1095: Stamens 6 1099

1096 Perianth segments united at base *(1095)* 1097

1096: Perianth segments free 1098

1097 Anthers with transverse dehiscence *(1096)* .... **Burmanniaceae**

1097: Anthers with longitudinal dehiscence .... **Iridaceae**

1098 Ovules 1 or 2 per loculus *(1096:)* .... **Haemodoraceae**

1098: Ovules usually several per loculus .... **Iridaceae**

1099 Plant a colourless saprophyte *(1095:)* 1100

1099: Plant chlorophyllous 1101

1100 Perianth actinomorphic *(1099)* .... **Burmanniaceae**

1100: Perianth zygomorphic .... **Corsiaceae**

1101 Leaf margins serrate *(1099:)* .... **Bromeliaceae**

1101: Leaf margins entire 1102

1102 The two perianth whorls different in texture and/or colour *(1101:)* .... **Bromeliaceae**

1102: Perianth segments all similar in texture and colour 1103

1103 Flowers in umbels, rarely solitary on a leafless scape *(1102:)* .... **Liliaceae**

1103: Flowers in simple or compound racemes 1104

1104 Leaves narrow, up to 20 cm long, arising from an underground rhizome *(1103:)* .... **Liliaceae**

1104: Leaves thick, fibrous, up to 2 m long, in tufts at base or apex of trunk-like stem .... **Agavaceae**

GLOSSARY

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This glossary contains terms used in all volumes of the *Flora of Australia*, but with particular reference to the flowering plant volumes (Vols 2–50). It includes terms defined in the Supplementary Glossaries of each volume published up to 1998. Some general terms used for other groups are included. Specialised glossaries for the ferns, gymnosperms and their allies will appear in *Flora of Australia* Vol. 48, for bryophytes in *Flora of Australia* Vol. 51 and for lichens in *Flora of Australia* Vol. 54. Specialised terms required only for particular volumes or families will continue to be inserted as required as Supplementary Glossaries in future volumes. A consolidated, continually updated, version of this Glossary is available on the ABRS Website.

Where alternative terms are given, the unbracketted alternative is the preferred terminology for use in *Flora of Australia*.

abaxial: *of the side or surface of an organ,* facing away from the axis. cf. **adaxial**.

abscission: the normal shedding from a plant of an organ that is mature or aged, e.g. a ripe fruit, an old leaf. adj. **abscissile**.

acarodomatia: domatia adapted to provide shelter to beneficial mites.

accessory fruit: a fruit, or group of fruits derived from one flower, in which the conspicuous, fleshy portion develops from the receptacle and is shed with the true fruit(s) attached.

accrescent: continuing to increase in size after maturity, as the calyx of some plants after flowering.

accumbent: *of the orientation of an embryo*, with the radicle lying against the edges of the two cotyledons.

achene: a dry, indehiscent fruit formed from a superior ovary of one carpel and containing one seed which is free from the pericarp (often applied, less correctly, to the one-seeded fruits of Asteraceae). cf. **cypsela**.

acicle: a slender, stiff, needle-like prickle. adj. **acicular**. Fig. 126B.

aciculate: finely scored on the surface, as if scratched by a pin.

acrodromous: with two or more primary or strongly developed secondary veins running in convergent arches towards the leaf apex. Arches not recurved at base.

acropetal: arising or developing in a longitudinal sequence beginning at the base and proceeding towards the apex. cf. **basipetal**.

acrostichoid: *of sporangia*, densely covering the abaxial surface of the fertile frond, i.e. not in distinct groups; *of ferns*, having the sporangia arranged as above.

acrotonic: *of flowering seasonal growth units (seasonal shoots)*, producing leaves below the inflorescence, cf. **basitonic.**

actinomorphic: *of flowers*, radially symmetrical; symmetrical about more than one plane passing through the axis of the flower. cf. **peloric**, **zygomorphic**.

aculeate: prickly.

acumen: a long, tapering point.

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acuminate: tapering gradually to a protracted point. Fig. 126Y.

acute: terminating in a distinct but not protracted point, the converging edges separated by an angle less than 90°. Fig. 126Z.

adaxial: facing towards the axis. cf. **abaxial**.

adnate: fused to an organ of a different kind, e.g. applied to a stamen fused to a petal.

adventitious: arising in abnormal positions, e.g. roots arising from the shoot system, buds arising elsewhere than in axils of leaves.

adventive: introduced to an area recently. cf. **introduced**, **naturalised**.

aerenchyma: tissue incorporating large, gas-filled spaces interspersed with the cells in a characteristic pattern.

aestivation: the arrangement of sepals and petals or their lobes in an unexpanded flower bud. cf. **vernation**. Fig. 136A–D.

aggregate fruit: a cluster of fruits formed from the free carpels of one flower. cf. **syncarp**.

albumen: = **endosperm**.

allantoid: sausage-shaped.

allopatric: *of two or more taxa,* having different ranges of distribution. cf. **sympatric**.

alternate: *of leaves or other lateral organs,* borne singly at different heights on the axis; *of floral parts,* on a different radius, e.g. describing the position of stamens with respect to petals. cf. **opposite**. Fig. 130K, L.

alternitepalous: *of floral parts*, inserted alternately with the tepals.

alveolate: pitted or honeycombed on the surface.

amplexicaul: *of a leaf base*, stem-clasping. Fig. 128C.

anastomosis: fusion to form a network, e.g. of veins in a leaf blade.

anatropous: *of an ovule*, inverted so that the micropyle faces the placenta. Fig. 136L.

anauxotelic: applied to inflorescences, parts of inflorescences or to axes that do not end in a flower, and in which growth does not continue beyond the flowering region, cf. **auxotelic.**

androdioecious: having bisexual flowers and male flowers, on separate plants.

androecium: the stamens of one flower collectively.

androgynophore: a stalk bearing both the androecium and gynoecium of a flower above the level of insertion of the perianth.

androgynous: having male and female flowers in the same inflorescence.

andromonoecious: having bisexual and male flowers, on the same plant.

androphore: a stalk bearing the androecium.

anemophilous: pollinated by wind.

angiosperm: a seed-bearing plant whose ovules, and hence seeds, develop within an enclosed ovary. cf. **gymnosperm**.

angustiseptate: with narrow partitions, cf. **latiseptate**.

annual: a plant whose life span ends within one year after germination.

annular: arranged in or forming a ring.

annular corona: raised fleshy tissue, usually in a ring, on the corolla around the base of the staminal column but not closely adnate to it.

annulus: a ring; *in ferns*, the elastic ring of cells, forming part of the sporangium wall, that initiates dehiscence.

anterior: *of floral organs*, on the side of the flower farthest from the axis. cf. **posterior**.

anther: the pollen-bearing part of a stamen. cf. **filament**. Fig. 132A–I.

antheridium: the fertile organ of a male gametophyte or the male organ of a bisexual gametophyte, in which male gametes are formed.

anthesis: the time of opening of a flower.

anthocarp: a false fruit consisting of the true fruit and the base of the perianth, as in Nyctaginaceae.

anticous: anterior, at the front, i.e. close to the leading or distal edge of the leaflet.

antipetalous: inserted in front of the petals; opposite the petals.

antisepalous: inserted in front of the sepals; opposite the sepals.

antrorse: bent, and pointing towards the apex. cf. **retrorse**.

apetalous: without petals.

apical: *of a placenta*, at the top of the ovary. Fig. 136J.

apiculum: a short, abrupt, flexible point, adj. **apiculate**. Fig. 126CC.

apocarpous: *of a gynoecium*, consisting of two or more carpels which are free from one another or almost so.

apomict: a plant that produces viable seed without fertilisation.

appendage: a structure arising from the surface or extending beyond the tip of another structure.

appressed: pressed closely against a surface (or another organ) but not united with it.

aquatic: living in or on water for all or a substantial part of the life span (generally restricted to fresh/inland waters).

arborescent: resembling a tree (applied to non-woody plants attaining tree height and to shrubs tending to become tree-like in size). cf. **dendroid**.

arcuate: curved like a bow.

areole: a space between the threads of a net; *in Cactaceae*, a cluster of hairs/spines/bristles borne at the node of a leafless stem; *in Mimosaceae (for example)*, a distinct, oblong or elliptical area on the face of a seed, bounded by a fine line; *on leaf laminas:* the space bounded by the finest veins. adj. **areolate**.

aril: a structure partly or wholly covering the testa of a seed and formed by expansion of the funicle. adj. **arillate**.

aristate: having a stiff, bristle-like awn or tip. Fig. 126W.

aristulate: having a small awn.

article: a segment of a jointed stem, or of a fruit with constrictions between the seeds.

articulate: jointed; having joints where separation may occur naturally; *of a stem*, having nodes.

ascending: growing erect after an oblique or semi-horizontal beginning.

asexual: not forming part of a cycle which involves fertilisation and meiosis.

asperulate: slightly rough to the touch.

attenuate: tapering gradually.

auricle: an ear-shaped appendage at the base of a leaf, leaflet or corolla lobe. adj. **auriculate**. Fig. 126T.

autapomorphic: *of a character*, derived and unique to a given taxon or monophyletic group.

autochthonous: *of the inhabitants of a region*, original; earliest known; (applied to an element of the Australian flora rich in endemics and believed to have been evolving in Australia for a long period of time).

autotrophic: independent of other organisms in respect of organic nutrition; able to fix carbon dioxide, by photosynthesis, to form carbohydrates.

auxotelic: applied to inflorescences, parts of inflorescences or to axes that do not end in a flower, and in which growth continues beyond the flowering region, cf. **anauxotelic.**

awn: a bristle-like appendage, e.g. on the tip or back of the lemma of a grass floret.

axil: the angle between a leaf or bract and the axis bearing it. adj. **axillary**. Fig. 133B.

axile: on an axis; *of a placenta*, on the central axis of the ovary. Fig. 136E.

axis: a stem, (commonly used for the main stem of a whole plant or of an inflorescence).

baccate: berry-like; *of seeds*, having a succulent or pulpy testa; *of fruits*, having the seeds embedded in pulp.

barbed trichome: a trichome with terminal or lateral retrorse projections, each projection being a barb. Fig. 139G.

barbellae: short, straight, stiff hairs or barbs.

barbulae: in *Scaevola* (Goodeniaceae), outgrowths on the margin of the wings or in the throat of the corolla, sometimes with apical hairs or papillae.

basal: at the base; *of a placenta*, at the base of the ovary. Fig. 136I.

basifixed: attached at or by the base, e.g. *of anthers*, by the base of the connective. cf. **medifixed**, **versatile**.

basipetal: developing, in sequence, from the apex towards the base. cf. **acropetal**.

basiscopic: *of the first lateral vein of a leaflet on the side nearer the leaf base*, pointing towards the base.

basitonic: *of flowering seasonal growth units (seasonal shoots)*, producing no leaves (but sometimes some bracts) below the inflorescence, cf. **acrotonic.**

beak: a prominent terminal projection, especially of a carpel or fruit.

beard: a tuft, line or zone of hairs. Fig. 138J.

berry: a fleshy or pulpy indehiscent fruit with the seed(s) embedded in the fleshy tissue of the pericarp. cf. **drupe**, **pyrene**.

biennial: a plant whose life span extends for more than one but less than two years after germination.

bifacial: *of leaves*, flat or channelled with distinct adaxial and abaxial surfaces.

bifid: divided, for about half the length, into two parts. cf. **bipartite**.

bifid trichome: a trichome divided into two branches. Fig. 139H.

bifoliate: *of plants*, having two leaves.

bifoliolate: *of leaves*, having two leaflets.

bigeminate: in two pairs; *of pinnate leaves,* having only two pairs of pinnae.

bilabiate: two-lipped, e.g. of a corolla in which fusion of an anterior group and a posterior group of petals extends beyond the top of the corolla tube.

bilamellate: consisting of two plates or lamellae.

bilocular: having two cavities.

bipartite: divided, nearly to the base, into two parts. cf. **bifid**.

bipinnate: *of leaves*, twice pinnately divided. cf. **pinnate**, **tripinnate**. Fig. 127N.

biseriate: arranged in two rows or whorls.

bisexual: bearing both male and female organs together, e.g. on the same gametophyte or in the same flower.

biternate: twice ternate, the three pinnae each divided into three pinnules. Fig. 127K.

blade: the expanded part of a leaf or petal. cf. **lamina**, **limb**.

bole: the trunk of a tree, below the lowest branch. cf. **canopy**.

brachyblast: a short branch; a spur shoot.

bract: a leaf-like structure, different in form from the foliage leaves and without an axillary bud, associated with an inflorescence or flower.

bracteole: a small bract-like structure borne singly or in pairs on the pedicel or calyx of a flower.

branched trichome: trichome divided into two or more branches. Fig. 139H–J.

bristle: a rigid trichome similar to a pig's bristle. Fig. 139D.

brochidodromus: pinnate venation in which the secondary veins do not terminate at the margins but are joined in a series of prominent arches.

bulb: a storage organ, usually underground, made up of a stem and leaf bases, the food reserves being stored in the inner, fleshy leaf bases.

bulbel (= **bulblet**): a bulb arising from another bulb.

bulbil: a small, deciduous bulb (or tuber) formed in the axil of a leaf or replacing flowers in an inflorescence, and functioning to propagate the plant vegetatively. Fig. 125E.

bullate: having a blistered or puckered surface; *of a leaf surface*, prominently raised (like a bubble) between veins.

burr: a rough or prickly propagule consisting of a seed or fruit and associated floral parts or bracts.

buttress: a flange of tissue protruding from the base of the main trunk of a tree.

caducous: falling off early.

caespitose: growing in tufts.

callus: a protruding mass of hardened tissue, often formed after an injury but sometimes a regular feature of the plant, e.g. on the labellum of some orchids and on the axis of the spikelet of some grasses. adj. **callose**; pl **calli**.

calycine: belonging to the calyx; with a well-developed calyx.

calyptra: *in mosses*, a cap-like structure covering or partly covering the capsule and derived from the neck of the archegonium; *in a flower*, (= operculum), a cap formed by fusion or cohesion of perianth parts and covering the stamens and carpels in the bud.

calyx tube: a tube formed by fusion or cohesion of sepals. cf. **hypanthium**.

calyx: the sepals of one flower collectively.

campanulate: bell-shaped.

campylotropous: *of an ovule*, orientated transversely (i.e. with its axis at right angles to its stalk) and with a curved embryo sac. Fig. 136M.

canaliculate: with a longitudinal groove or channel.

canescent: more or less grey-pubescent, hoary.

canopy: the branches and foliage of a tree. cf. **bole**.

capillary: *of hairs etc*., very slender.

capitate: *of an inflorescence*, with the flowers unstalked and aggregated into a dense cluster; *of a stigma*, globose, like the head of a pin.

capitellate: shaped like, or aggregated into, a very small head.

capitulum (= head): a dense cluster of sessile flowers. adj. **capitate**. Fig. 133F.

capsule: a dry fruit formed from two or more united carpels and dehiscing at maturity to release the seeds. Figs 133J–M, 134C, D.

carinate: keeled.

carpel: an organ (generally believed to be a modified foliar unit) at the centre of a flower, bearing one or more ovules and having its margins fused together or with other carpels to enclose the ovule(s) in an ovary, and consisting also of a stigma and usually a style.

carpophore: *in ferns*, the stalk of a sporocarp; *in a fruit*, the stalk of a mericarp.

caruncle (= **strophiole**): an outgrowth of a seed coat, near the hilum.

caryopsis: a dry, indehiscent, one-seeded fruit in which the seed coat is closely fused to the fruit wall (characteristic of grasses).

cataphyll: a scale leaf associated with a vegetative propagating organ such as a rhizome or perennating bud; a simple, scale-like leaf.

catkin: a spike in which the flowers are unisexual and without conspicuous perianth.

caudate: having a narrow tail-like appendage. Fig. 126X.

caudex: a thick, erect trunk, especially of cycads.

caudicle: a thread to which a pollen mass is attached in Orchidaceae and Asclepiadaceae; the part of a pollinarium that connects the corpusculum with the pollinia.

cauliflorous: *of plants*, with flowers (and fruits) borne on a well-developed trunk or major branch. cf. **cauline**. Fig. 133E.

cauline: *of leaves*, borne on an aerial stem; *of flowers or fruits*, borne on old wood. cf. **cauliflorous**).

cell: the basic unit of plant structure consisting, at least when young, of a protoplast surrounded by a wall.

centrifugal: directed, or developing, from the centre or axis outwards.

centripetal: directed, or developing, from the outside towards the centre or axis.

chaff: thin, dry unfertilised ovules among the fully developed seeds of a fruit; thin, membranous scales or bracts. Fig. 137A.

chalaza: the part of an ovule to which the end of the stalk (funicle) is attached.

chartaceous: papery.

chasmogamous: pollinated when the flower is open. cf. **cleistogamous**.

chlorophyll: pigment(s) constituting the green colouring matter of plants and absorbing radiant energy in photosynthesis.

chromosome: a thread-like structure in the nucleus of a cell, containing a linear sequence of genes.

cilia: *in gametes, spores etc.*, minute hair-like protoplasmic protrusions whose movement confers motility on the cell; *in vascular plants*, hairs more or less confined to the margins of an organ. sing. cilium; adj. **ciliate**. Fig. 139A.

ciliolate: minutely ciliate.

cincinnus: a monochasial, cymose inflorescence with flowers arising alternately from one side of an axis then the other.

cinereous: ash-grey, as of wood ash.

circinnate (= **circinate**)**:** spirally coiled, with the tip innermost.

circumsciss: (to) break open along a transverse line around the circumference. adj. **circumscissile**. Fig. 133J.

cladode: the photosynthetic stem of a plant whose foliage leaves are absent or much reduced. cf. **phyllode**.

cladophyll: a flattened, leaf-like photosynthetic stem not bearing leaves or scales. cf. **phylloclade**.

class: a major taxonomic rank, between order and division.

clathrate: latticed or pierced with apertures like a trellis.

clavate: club-shaped.

claw: a narrow, stalk-like basal portion of a petal, sepal or bract.

cleistogamous: self-pollinated and setting fertile seed but the flowers never opening. cf. **chasmogamous**.

clone: a set of organisms produced from one parent by vegetative reproduction.

cobwebbed: covered with long, weak, loosely entangled, thin hairs, resembling spiderwebs; usually white. Fig. 137B.

coccus: a one-carpel unit of a schizocarp or lobed fruit, becoming separate at maturity. pl. **cocci**.

cochlear: *of the arrangement of corolla lobes in a bud*, a variant of imbricate aestivation. Fig. 136A.

cochleate: coiled like a snail-shell.

cohesion: the sticking together of floral parts of the same whorl without organic fusion. adj. **coherent**.

collateral: situated side by side; adjacent and on the same radius of an axis.

colleter: a group or tuft of mucilaginous secretory hairs, often found near the base of the leaf lamina and on the calyx in Apocynaceae and Asclepiadaceae.

colliculate: covered with small, rounded or hillock-like elevations (n. **colliculae**). Fig. 134M.

colpate: *of a pollen grain*, having elongate apertures.colporate: *of a pollen grain*, having apertures with pores within colpi. cf. **porate**.

columella: a little column; the central, persistent axis of a schizocarpic fruit; the axis of a cone or cone-like fruit.

column: the lower part of an awn in grasses, when distinctly different in form from the upper part; (= **gynostemium**) a structure in Orchidaceae, Asclepiadaceae and Stylidiaceae, extending above the ovary of a flower and incorporating stigma, style and stamens.

coma: a tuft, especially of hairs on a seed. adj. **comose**. Fig. 138K.

commissure: a join or seam; the interfacing of two fused carpels in an ovary.

complicate: *of leaves*, the lamina (or part of the lamina) folded upon itself.

compound: *of a leaf*, having the blade divided into two or more distinct leaflets; *of an inflorescence*, made up of an aggregate of smaller inflorescences.

compressed: flattened in one plane, either dorsally (bringing the front and back closer together) or laterally (bringing the sides closer together).

concolorous: coloured uniformly; the same colour on both sides. cf. **discolorous**.

conduplicate: folded together, with the fold-line along the long axis (e.g. *of cotyledons in a seed*).

cone: *in gymnosperms and club-mosses*, a group of sporophylls arranged compactly on a central axis; (loosely) *in Casuarinaceae*, a woody multiple fruit incorporating the bracts and bracteoles associated with the flowers; (loosely) *in Petrophile and other Proteaceae* the semi-woody multiple fruit made up of nutlets in the axils of closely imbricate floral bracts which become woody.

conflorescence: a compound inflorescence consisting of two or more unit inflorescences, in which the main axis does not end in a flower but the axes of the branches do so.

connate: fused to another organ (or other organs) of the same kind. Fig. 128G.

connective: the part of an anther that connects the lobes.

connivent: coming into contact; converging.

contorted: see convolute.

convolute: *of the arrangement of corolla lobes in a bud*, a form of imbricate aestivation in which each segment has one edge overlapping the adjacent segment, like a furled umbrella. Fig. 136C.

cordate: *of a leaf blade*, broad and notched at the base; heart-shaped (in two dimensions). Fig. 126Q.

cordiform: shaped like a heart (in three dimensions).

coriaceous: leathery.

corm: a fleshy, swollen stem base, usually underground, in which food reserves are stored between growing seasons.

corniculate: bearing, or terminating in, one or more small horns.

corolla: the petals of a flower collectively.

corolline corona: fleshy ridges or outgrowths of tissue attached to the corolla tube, usually in the lobe sinuses.

corona: a ring of tissue arising from the corolla, perianth or filaments of a flower and standing between the perianth lobes and the stamens.

corpusculum: the central part of a pollinarium.

cortex: the region of a stem or root surrounding the vascular cylinder but inside the epidermis.

corymb: a racemose inflorescence in which the pedicels of the lower flowers are longer than those of the flowers above, bringing all flowers to about the same level. Fig. 131G.

costa: a rib; a midrib or middle-nerve (when it is the only nerve).

costate: ribbed.

costule: the midvein of a pinnule.

cottony: with long, soft, weak, filamentous hairs, somewhat flocculent and entangled, like the cotton of *Gossypium* seeds. Fig. 137C.

cotyledon: the primary leaf (or one of two or more primary leaves) of an embryo.

crenate: with small, rounded teeth; scalloped. Fig. 127T.

crenulate: minutely scalloped. Fig. 127U.

crisped: curled.

crown: the part of a tree or shrub above the level of the lowest branch.

crownshaft: *in palms*, a conspicuous cylinder formed by the tubular base of leaf sheaths at the top of a stem.

crustaceous: brittle.

cryptogam: (literally) a plant whose sexual reproductive parts are not conspicuous; a plant that produces spores, not seeds, in its sexual reproductive cycle; *among vascular plants*, ferns and fern allies. cf. **phanerogam**.

cucullate: hooded; hood-shaped.

culm: an aerial stem; *in grasses, sedges, rushes, etc.*, the stem bearing the inflorescence.

cuneate: wedge-shaped. Fig. 126N.

cupule: a small cup.

cupuliform: nearly hemispherical, shaped like a cupola (dome).

curvinerved: with curved parallel veins.

cushion, floral: a swollen floral axis on which several small flowers are borne.

cuspidate: tapering into a sharp, rigid point. Fig. 126AA.

cyathium: an inflorescence of unisexual flowers surrounded by a cup of involucral bracts, as in *Euphorbia*.

cyclic: *of floral organs*, several borne at the same level on the axis; whorled. cf. **spiral**.

cyme: an inflorescence in which each flower, in turn, is formed at the tip of a growing axis and further flowers are formed on branches arising below it. adj. **cymose**. cf. **raceme**. see also **dichasial cyme**, **monochasial cyme**. Fig. 131E, F.

cymule: a diminutive cyme, usually few-flowered.

cypsela: a dry, indehiscent, one-seeded fruit formed from an inferior ovary. cf. **achene**.

cystolith: a stalked structure growing from a cell wall into the cell cavity, encrusted with calcium carbonate.

deciduous: falling seasonally, e.g. of the leaves or bark of some trees. cf. **evergreen**.

declinate: angled downwards or forwards. cf. **decurved**.

decompound: more than once compound.

decumbent: spreading horizontally but then growing upwards.

decurrent: extending downwards beyond the point of insertion, e.g. of a lamina extending downwards to form a flange along the petiole.

decurved: angled downwards and curved or curled.

decussate: in opposite pairs, with successive pairs borne at right angles to each other.

definite: of a constant number; *of stamens*, twice as many as the petals or sepals, or less; *of an inflorescence*, ending in a flower or an aborted floral bud.

deflexed: bent abruptly downwards. cf. **inflexed**.

dehiscent: breaking open at maturity to release the contents. Figs 132A–E, 133J–M.

deltoid (= **deltate**): triangular with the sides of about equal length. Fig. 126L.

dendritic: *of a trichome*, with branches arising along the main axis, i.e. tree-like. Fig. 139I.

dendroid: tree-like in form but not in size. cf. **arborescent**.

dentate: toothed. Fig. 127R.

denticle: a small tooth; in *Coprosma* (Rubiaceae), thick papillate tubercles on the margin of the interpetiolar stipules. Fig. 133K.

denticulate: finely toothed. Fig. 127S.

depressed: flattened as if pressed down from the top or end.

determinate: *of growth or branching*, with a bud or flower terminating the growth of the main axis; *of an inflorescence*, see definite.

dextrorse: turned towards the right. cf. **sinistrorse**

diadelphous: having the stamens united into two groups, or all but one united in a group and one free.

diaphanous: extremely thin and transparent.

dichasium: a cymose inflorescence with opposite branching below the flower which terminates each axis. pl. **dichasia**. cf. **monochasium**.

dichasial cyme: an inflorescence composed of dichasia. Fig. 131E.

dichlamydeous: *of a flower*, having two whorls of perianth parts.

dichotomous: forking into two equal branches resulting from division of the growing point.

diclinous: having the stamens and the carpels in separate flowers.

dicotyledon: a flowering plant whose embryo has two (rarely more) cotyledons (seed leaves). cf. **monocotyledon**.

didymous: borne in pairs; *of anthers*, having two lobes, with scarcely any tissue connecting them.

didynamous: *of stamens*, four in number, two being distinctly longer than the other two.

digitate: branching from the axis or stalk like the fingers of a hand. Fig. 127H.

dimidiate: appearing to be halved, as when half an organ is so much smaller than the other that it seems absent.

dimorphic: of two different forms.

dioecious: having the male and female reproductive structures on separate plants. cf. **monoecious**.

diplecolobous: *of cotyledons in a seed*, twice folded transversely.

diploid: having two of the basic sets of chromosomes in the nucleus. cf. **haploid**, **polyploid**.

diplostemonous: with stamens in 2 whorls.

disc: a plate or rim of tissue, derived from the receptacle of a flower, occurring between whorls of floral parts.

discolorous: of different colours; *of leaves*, having the two surfaces different in colour; variegated. cf. **concolorous**.

dissepiment: a partition (septum) within an ovary or fruit, derived by fusion of adjacent carpels.

distal: remote from the point of origin or attachment. cf. **proximal**.

distichous: arranged in two rows on opposite sides of a stem and thus in the same plane. Fig. 130L.

diurnal: *of flowers*, opening only during daylight hours.

divaricate: widely spreading and often ±horizontal.

divergent: of like structures spreading widely but separating by degrees from axis, attachment, or point of reference and from each other, e.g. branches of pappus of *Carthamnus lanatus*.

division: the major taxonomic rank within the Plant Kingdom. Alternative name for **phylum**.

domatia: small structures on the lower surface of a leaf in some woody dicotyledons, located in the axils of the primary veins and usually consisting of depressions partly enclosed by leaf tissue or hairs. sing. **domatium**. Fig. 125A–C.

dorsal: *of a lateral organ*, (relating to the side) facing away from the axis, i.e. the 'back'; *of a thallus*, facing away from the substratum. cf. **ventral**.

dorsifixed: attached at or by the back.

dorsiventral: having structurally different upper and lower surfaces.

drupe: a succulent fruit formed from one carpel, having the seed(s) enclosed in an inner stony layer of the fruit wall. adj. **drupaceous** (which is often used to mean drupe-like but not strictly a drupe). cf. **berry**, **pyrene**.

duplicate: folded twice.

echinate: bearing stiff, stout, prickly hairs. Fig. 134K.

edaphic: pertaining to the soil.

eglandular: without glands.

elaiosome: an appendage of a seed, usually rich in oil, attractive to fauna (especially ants) and hence an aid to dispersal by such fauna.

elater: in *Equisetum,* an appendage to the spore.

elliptic: oval in outline, widest at the centre. Fig. 126H.

emarginate: having a broad, shallow notch at the apex. Fig. 126FF.

embryo: a young plant contained within an archegonium or seed.

emersed: *of leaves, flowers, etc.*, rising above the surface of water in which the plant is rooted.

enation: an epidermal outgrowth.

endemic: having a natural distribution confined to a particular geographical region.

endocarp: the innermost layer of the wall of a fruit; *in a drupe*, the stony layer surrounding the seed.

endosperm: nutritive tissue in a seed, in angiosperms triploid and formed in the embryo sac after fertilisation, in gymnosperms haploid and derived from the sterile portion of the female gametophyte. cf. **perisperm**.

ensiform: sword-shaped.

entire: having a smooth margin, not dissected or toothed. Fig. 127O.

entomophilous: pollinated by insects.

ephemeral: short-lived.

epicalyx: a whorl of bracts, just below a flower, looking like a second calyx.

epicarp: the outer layer of the wall of a fruit, i.e. the 'skin'. Also known as the exocarp.

epicormic: *of buds, shoots or flowers*, borne on the old wood of trees (applied especially to shoots arising from dormant buds after injury or fire).

epicortical: on top of the bark, i.e. outside the bark.

epidermis: the outermost layer of cells of an organ, usually only one cell thick.

epigeal: *of germination*, having the cotyledon(s) emerging from the seed coat and becoming photosynthetic. cf. **hypogeal**.

epigynous: *of floral parts (especially stamens)*, attached above the level of insertion of the ovary, and arising from tissue that is fused to the ovary wall. cf. **hypogynous**, **perigynous**. Fig. 135D, E.

epipetalous: borne on the petals. Fig. 135C.

epiphyllous: growing on leaves, e.g. the vegetatively derived plantlets of some Crassulaceae; *of bryophytes, lichens, fungi*, growing upon leaves but not parasitic on them.

epiphyte: a plant growing on, but not parasitic on, another plant (often loosely applied to plants, such as orchids, that grow on vertical rock faces). cf. **parasite**, **saprophyte**.

episepalous: *of stamens*, borne on the sepals.

equilateral: *of stamens*, with anthers regularly spaced around the style.

equitant: *of a leaf*, folded in half along the midline so that the adaxial surface disappears from view, and overlapping the edges of a similarly folded leaf on the opposite side of the stem (at least at the base).

eremean: belonging to regions of low, irregular rainfall.

erose: *of a margin*, finely and irregularly eroded or incised.

eucamptodromous: pinnate venation in which the secondary veins do not terminate at the margins but which gradually diminish inside the margin, connected to the superadjacent secondary veins by a series of cross-veins without forming prominent marginal loops.

eusporangiate: *of ferns*, having sporangia with walls more than one cell thick. cf. **leptosporangiate**.

evergreen: bearing green leaves throughout the year. cf. **deciduous**

excentric: to one side; off centre.

exine: the outer layer of the wall of a pollen grain or spore.

exocarp (= **epicarp**)**:** the outer layer or "skin" of a pericarp.

exserted: protruding, e.g. of stamens with respect to a corolla tube.

exstipulate: without stipules.

extrafloral: *of nectaries*, not within the flower.

extrastaminal: outside the stamens.

extravaginal: *of a shoot*, arising from an axillary bud which breaks through the sheath of the subtending leaf.

extrorse: *of anthers*, opening away from the centre of the flower. cf. **introrse**.

facultative: *of parasites*, optional. cf. **obligate**.

falcate: sickle-shaped. Fig. 126F.

family: a group of one to many genera believed to be related phylogenetically, usually clearly separable from other such groups; the major taxonomic group between genus and order.

farinaceous: containing starch grains; mealy; resembling flour.

fascicle: a cluster, adj. **fasciculate**.

favulariate: *of a surface*, finely ribbed, the ribs separated by zig-zag furrows.

felted: covered with very dense, interlocked and matted trichomes having the appearance or texture of felt or woollen cloth, cf. tomentose. Fig. 137D.

fenestrate: having openings or translucent areas ('windows').

fertilisation: the union of male and female gametes.

filament: the stalk of a stamen; a thread one or more cells thick.

filiform: thread-like. Fig. 126C.

fimbriate: *of a margin*, fringed with long slender hair-like processes (called fimbriae). Fig. 139B.

fimbrillate: minutely fimbriate.

fistular: hollow throughout its length.

flabellate (= flabelliform): fan-shaped.

flaccid: limp; tending to wilt. cf. **turgid**.

flagelliform: long and very slender, like a whip-lash.

flexuose (= **flexuous**)**:** bent from side to side in a zig-zag form.

floccose: bearing tufts of soft hairs or wool which tend to rub off and adhere in small masses. Fig. 137E.

floral: belonging to or associated with a flower.

floret: a grass flower, together with the lemma and palea that enclose it (often also applied to the individual small flowers in Cyperaceae and Asteraceae).

flower: the sexual reproductive structure of the angiosperms, typically consisting of gynoecium, androecium and perianth and the axis bearing these parts.

foliaceous: leaf-like.

follicle: a dry, dehiscent fruit formed from one carpel and dehiscing along the line of fusion of its edges. Fig. 134B.

forb: a non-woody plant other than a grass, sedge, rush, *etc.* cf. **herb**.

-form: superficially resembling; e.g. umbelliform (inflorescence resembling but not truly an umbel).

foveate: pitted. Fig. 134F.

free-central: *of placentation,* with the ovules borne on a free-standing central placenta within the ovary. Fig. 136F.

free: *of floral organs,* not fused or united with other similar organs.

frond: a leaf, especially of a fern, cycad or palm.

fruit: the seed-bearing structure in angiosperms, formed from the ovary after flowering.

frutescent: becoming shrub-like (woody).

fruticose: shrub-like.

fugacious: falling or withering away very early.

fulvous: dull yellowish brown or yellowish grey.

funicle (= **funiculus**)**:** the stalk of an ovule.

fusiform: spindle-shaped, i.e. narrower at both ends than at the centre.

gamete: a cell or nucleus that fuses with another, of opposite sex, in sexual reproduction.

gametophyte: a plant, or phase of a plant's life cycle, that bears gametes.

gamopetalous: see sympetalous.

gamophyllous: having the leaves or perianth segments united by their margins, at least at the base.

gamosepalous: having the sepals united by their margins, at least at the base.

gemma: a bud or bud-like organ capable of reproducing the plant. *pl.* **gemmae**.

geniculate: bent abruptly like a knee joint.

genotype: the total complement of hereditary factors (genes) acquired by an organism from its parents and available for transmission to its offspring. cf. **phenotype**.

genus: a group of species believed to be related phylogenetically and usually clearly separable from other such groups, or a single species without close relatives; the major taxonomic rank between species and family. pl. **genera**.

geophyte: a plant whose perennating buds are buried in the soil.

gibbous: *usually of a calyx or corolla,* with a large hump or pouch-like swelling.

glabrate: glabrous, but obviously having previously had an indumentum.

glabrescent: becoming glabrous.

glabrous: without hairs.

gland: a structure, within or on the surface of a plant, with a secretory function.

glandular: bearing glands; functioning as a gland.

glandular trichome: trichome terminating in a gland or functioning as a secretory organ or accumulatory organ. Fig. 139C.

glaucous: blue-green in colour, with a whitish bloom (as in the juvenile leaves of many *Eucalyptus* species).

globose: nearly spherical.

glochid: a barbed hair or bristle.

glomerule: a small compact cluster. adj. **glomerulate**. Fig. 133G.

glumaceous: glume-like, tending to be chaffy or membranous in texture.

glume: a bract in the inflorescence of a grass, sedge or similar plant.

grain: a fruit characteristic of grasses (= **caryopsis**); pollen grain, a microspore of a seed plant, or the partially developed gametophyte formed from it.

granulate: *of a surface*, granular.

guard cells: the two cells that open and close the stomata to allow gas exchange.

gymnosperm: a seed plant with the ovules borne on the surface of a sporophyll. cf. **angiosperm**.

gynobasic: *of a style*, arising near the base of the gynoecium, e.g. between the lobes of the ovary.

gynodioecious: having bisexual flowers and female flowers on separate plants. cf. **gynomonoecious**.

gynoecium: the carpels of a flower collectively.

gynomonoecious: having bisexual and female flowers on the same plant cf. **gynodioecious**.

gynophore: a stalk bearing the gynoecium above the level of insertion of the other floral parts.

gynostegial corona: collective term for the staminal and interstaminal coronas, both of which are associated with the gynostegium. cf. **interstaminal corona**, **staminal corona**.

gynostegium: a structure formed by the fusion of the stamens and the gynoecium in Asclepiadaceae. cf. **column**.

habit: the growth form of a plant, comprising its size, shape, texture and orientation.

habitat: the environment in which a plant lives.

hair: an elongate single-celled or multi-celled outgrowth from the epidermis, without vascular tissue.

half-inferior: *of an ovary*, partly below and partly above the level of attachment of the perianth and stamens. Fig. 135D.

halophyte: a plant adapted to living in highly saline habitats; a plant that accumulates high concentrations of salt in its tissues.

haploid: having a single set of chromosomes in the nucleus (i.e. having each gene locus represented only once).

hastate: spear-shaped; *of a leaf blade*, narrow and pointed but with two basal lobes spreading approximately at right angles. Fig. 126R.

haustorium: an absorbing organ through which a parasite obtains chemical substances from its host.

head: see capitulum. Fig. 133F.

helicoid: coiled; *of a cymose inflorescence*, branching repeatedly on the same side. cf. **scorpioid**.

hemiparasite: an organism which lives on and derives part of its nourishment from a different organism, and is partially self-supporting.

herb: any vascular plant that never produces a woody stem. cf. **forb**.

herbaceous: not woody; soft in texture.

hermaphrodite: = **bisexual**.

hesperidium: a fleshy indehiscent fruit derived from a single pistil, with an outer leathery rind and septate interior (e.g. *Citrus*).

heteroblastic: having the adult parts of the plant (especially the leaves) distinctly different in form from the juvenile parts.

heterogamous: producing flowers of two or more kinds with respect to their fertile organs, e.g. male and female or bisexual and female. cf. **homogamous**.

heteromorphic (= **heteromorphous**): of two or more distinct forms.

heterosporous: producing two kinds of spores (male and female, or microspores and megaspores). cf. **homosporous**.

heterostylous: species in which flowers are similar except that the stigmas and anthers are held at different levels relative to each other, because style length differs between plants. cf. **homostylous**.

hilum: the scar on a seed coat at the place where it was attached to its stalk during development.

hirsute: bearing coarse, rough, relatively long hairs. cf. **villous**. Fig. 137F.

hispid: bearing stiff, bristly hairs. Fig. 137G.

hispidulous: minutely hispid.

hoary: covered with a greyish layer of very short, closely interwoven hairs.

holotype: a single specimen or illustration designated by the author of a plant (or animal) name, at the time of original publication, which fixes the application of the name; the 'voucher specimen' of a name.

homogamous: having flowers of only one kind. cf. **heterogamous**.

homosporous: producing only one kind of spore in the sexual reproductive cycle, and hence one gametophyte which produces both male and female gametes. cf. **heterosporous**.

homostylous: species in which the flowers have stigmas and anthers held at the same level relative to each other on all plants. cf. **heterostylous**.

horizontal: lying in a plane parallel with the surface of the organ, usually applied when the organ is also oriented horizontally.

host: an organism on which a parasite lives and by which it is nourished (also applied, loosely, to a plant supporting an epiphyte).

hyalescent: becoming translucent.

hyaline: translucent, almost like clear glass.

hybrid: an offspring of genetically different parents (in a Flora, usually applied where the parents are of different species).

hygroscopic: absorbing water (and undergoing movements or changes brought about by changes in water content).

hypanthium: a cup or tube bearing floral parts above the base, and often above the top, of the ovary of a flower, e.g. in many Myrtales. cf. **calyx tube**.

hypocotyl: the part of the stem of an embryo or young seedling below the cotyledonary node.

hypodermis: a clearly differentiated layer of cells below the epidermis.

hypogeal: *of germination*, having the cotyledon(s) remaining within the seed coat. cf. **epigeal**.

hypogynous: arising below the level of insertion of the ovary (often applied, loosely, to a *flower* in which the sepals, petals and stamens are inserted below the ovary). cf. **perigynous**, **epigynous**. Fig. 135A, C.

imbricate: *of perianth parts*, having the edges overlapping in the bud. cf. **valvate**. Fig. 136A–C.

imparipinnate: having an uneven number of pinnae, by virtue of having one terminal pinna. cf. **paripinnate**. Fig. 127M.

incised: cut deeply, sharply and often irregularly (an intermediate condition between toothed and lobed). Fig. 127D.

included: enclosed, not protruding.

incrassate: thickened; *of a pollen grain*, with thickened margins around the apertures.

incumbent: *of the orientation of an embryo*, with the cotyledons lying face to face and folded downwards beside the radicle; *of anthers*, lying against the inner face of the filament.

incurved: bent or curved inwards or upwards; *of leaf margins*, curved towards the adaxial surface.

indefinite: variable in number; numerous; *of stamens*, more than twice as many as the petals or sepals; *of an inflorescence*, not terminating in a flower (i.e. having a continuing, terminal growing point).

indehiscent: not opening at maturity.

indeterminate (= **monopodial**)**:** *of growth*, the condition in which the terminal bud persists and produces successive lateral branches; *of an inflorescence*, when the floral axis is not terminated by a flower, ie a racemose inflorescence. cf. **cymose**.

indumentum: the epidermal appendages, e.g. hairs or scales, collectively. Figs 137, 138.

induplicate: folded inwards so that the outer faces of the margins are in contact.

indurated: hardened.

indusium: tissue covering the sorus of a fern; a hollow pollen-cup surrounding the stigma in Goodeniaceae.

inferior: *of an ovary*, at least partly below the level of attachment of the other floral parts. cf. **superior**. Fig. 135D, E.

inflexed: bent sharply upwards or forwards. cf. **deflexed**.

inflorescence: the group or arrangement in which flowers are borne on a plant.

infraspecific: of lower taxonomic rank than species.

infructescence: the grouping or arrangement in which fruits are borne on a plant.

insectivorous: catching, and ostensibly feeding on, insects.

inserted (*on*): attached to; arising from.

integument: a covering; one of the outer layers of tissue of an ovule.

intercalary: between two points. Fig. 133D.

intercalary growth: extension or growth from an **intercalary meristem**, i.e. neither from the apex nor the base.

intercalary inflorescence: an inflorescence that either arises in an internodal position, or one originally terminal but ceasing to be so when vegetative growth subsequently resumes from the stem apex. Fig. 133D.

internode: the portion of a stem between the level of insertion of two successive leaves or leaf pairs (or branches of an inflorescence).

interpetiolar: *of stipules*, between the petioles of two opposite leaves. cf. **intrapetiolar**.

interrupted: *of an inflorescence*, having the flowers unevenly distributed along the axis, with conspicuous gaps.

interstaminal corona: fleshy lobes, often connate into a tube, attached to the base of the staminal column in the interstaminal areas. cf. **gynostegial corona**.

intramarginal: situated inside but close to the margin, e.g. of a vein in a leaf.

intrapetiolar: between a petiole and the subtending stem. cf. **interpetiolar**.

introduced: not indigenous; not native to the area in which it now occurs. cf. **adventive**, **naturalised**.

introrse: *of anthers*, dehiscing towards the centre of the flower. cf. **extrorse**.

involucre: a group of bracts enveloping a condensed inflorescence; a layer of tissue enveloping particular structures, e.g. an archegonium in Bryophyta, sporangia in Hymenophyllaceae.

involucel: involucre of bractlets surrounding a secondary inflorescence such as the base of an umbellule.

involute: rolled inwards; *of a leaf*, with the margins rolled towards the adaxial surface. cf. **revolute**. Fig. 130C.

irregular: see zygomorphic.

isobilateral (= **isolateral**)**:** having structurally similar upper and lower surfaces.

isotype: a specimen which is a duplicate of the holotype, i.e. part of the same collection.

jugate: paired.

juvenile: *of leaves*, formed on a young plant and different in form from the adult leaves.

karyoevolution: evolutionary change in the chromosome set, expressed as changes in number and gross structure of the chromosomes; (more broadly), evolutionary relationships between taxa as indicated by karyotype differences.

karyotype: the gross morphology of the chromosome set, described in terms of number, length, centromere position, *etc*.

keel: a ridge like the keel of a boat; *in Fabaceae*, a boat-shaped structure formed by fusion of the two anterior petals of a flower.

keeled: *of leaves, petals or bracts*, folded and ridged along the midrib.

kwongan: low sand heath or sand plain sclerophyllous vegetation common in south-western W.A.

labellum: a lip; *in Orchidaceae*, the distinctive median petal that serves as an alighting platform for pollinating insects; *in Zingiberaceae and Costaceae*, a (usually showy) structure derived from petaloid staminodes.

laciniate: slashed into narrow, pointed lobes. Fig. 127E.

lacrymiform: tear-shaped, i.e. more or less ovoid or obovoid.

lacuna: a gap or cavity.

lamella: a thin, plate-like layer; middle lamella, the layer between the walls of two adjacent cells.

lamellose: composed of or arranged in layers or thin plates.

lamina: the blade of a leaf.

lanceolate: *of a leaf*, about four times as long as it is broad, broadest in the lower half and tapering towards the tip. Fig. 126G.

latex: a viscous fluid exuded from the cut surfaces of the leaves and stems of certain plants.

latiseptate: with broad partitions. cf. **angustiseptate**.

latrorse: turned sideways, i.e. not towards or away from axis; *of anthers*, opening laterally, i.e. towards adjacent anthers.

leaflet: one of the ultimate segments of a compound leaf.

lectotype: a specimen or illustration selected from among those cited with the original description to serve in place of a holotype where the holotype is missing or destroyed, or where no holotype was designated.

legume: a fruit characteristic of the families Mimosaceae, Caesalpiniaceae and Fabaceae, formed from one carpel and either dehiscent along both sides, or indehiscent; *in particular*, such a fruit that is grown as an edible crop; a crop species in the family Fabaceae.

lemma: the lower of two bracts enclosing a grass flower.

lenticel: a loosely-packed mass of cells in the bark of a woody plant, visible on the surface of a stem as a raised powdery spot, through which gaseous exchange occurs.

lenticular: shaped like a biconvex lens.

lepidote: covered with small, membranous scales.

leptosporangiate: *of ferns*, having sporangia with walls only one cell thick. cf. **eusporangiate**.

liane: a climbing or twining plant (usually applied to woody climbers).

lignified: woody, due to the deposition of lignin in cell walls.

lignotuber: a woody swelling at the base of the shoot system below or just above the ground, containing adventitious buds from which new shoots develop if the top of the plant is cut off or burnt (common in the shrubby eucalypts ('mallee') and in many other fire-tolerant Australian shrubs).

ligulate: bearing a ligule; strap-shaped.

ligule: a strap-shaped structure; a membranous or hairy appendage on the adaxial surface of a leaf, especially in grasses, at the junction between sheath and blade; a small adaxial appendage near the leaf base in some pteridophytes; the corolla limb in ray flowers of Asteraceae. Fig. 130 I.

limb: the upper, free, spreading portion of a corolla or perianth that is connate at the base.

linear: very narrow in relation to the length, and with the sides parallel. cf. **lorate.** Fig. 126D.

linguiform: tongue-shaped.

lithophyte: a plant that grows on the surface of unweathered rock.

lobulate: having small or indistinct lobes.

loculicidal: *of the dehiscence of a fruit*, along lines coinciding with the centres of loculi. cf. **septicidal**. Fig. 134D.

loculus: an enclosed compartment within an organ e.g. an ovary, an anther. pl. **loculi**.

lodicule: one of a pair of tiny scales in a grass floret, between the lemma and the fertile parts of the flower, which may be reduced perianth segments.

lomentum: a legume having distinct constrictions or lines of abscission between the seeds and breaking into one-seeded segments when mature.

lorate: *of leaves*, strap-shaped (moderately long with the two margins parallel). cf. **linear**.

lumen: the cavity of a plant cell.

lyrate: deeply lobed, with a large terminal lobe and smaller lateral ones. Fig. 127A.

macrospore: = **megaspore**.

mallee: a growth habit in which several woody stems arise separately from a lignotuber (usually applied to shrubby eucalypts); a plant having the above growth habit; vegetation dominated by such plants.

mammillate: having small nipple-shaped projections.

marcescent: withering without falling off.

marginal: occurring at or very close to the margin; *of a placenta*, on the (fused) margins of the carpel, i.e. along the suture. Fig.136H.

mealy: covered with meal-like or flour-like particles. Fig. 137H.

medifixed: attached by or at the middle, e.g. *of anthers*,with filament attached at the middle of the connective. cf. **basifixed**, **versatile**.

megagametophyte: a plant body or cell lineage, formed by vegetative growth of the megaspore, that produces the female gametes of a heterosporous plant.

megasporangium: the larger of the two kinds of sporangia produced in the sexual life cycle of a heterosporous plant.

megaspore: the larger of the two kinds of spores produced in the sexual life cycle of a heterosporous plant, giving rise to the female gametophyte.

megasporophyll: a specialised leaf upon which (or in the axil of which) one or more megasporangia are borne.

meiosis: the two-stage division of a diploid nucleus, occurring once in every sexual life cycle, in which gene recombination occurs and the number of chromosomes characteristic of the sporophyte plant is halved prior to the production of gametes.

mellitophily: an insect-flower pollination syndrome involving bees.

mentum: *in Orchidaceae*, a spur formed by extension of the base of the column.

mericarp: one segment of a fruit that breaks at maturity into units derived from the individual carpels. cf. **schizocarp**.

meristem: growing regions of a plant in which cells that have retained their embryonic characteristics, or have reverted to them secondarily, divide to produce new cells.

-mery: the number of parts per whorl that characterises a particular flower (generally constant for the perianth whorls and less often for the whorl(s) of stamens also). adj. **-merous**.

mesocarp: the fleshy portion of the wall of a succulent fruit inside the skin and outside the stony layer, if any, surrounding the seed(s).

mesophyll: photosynthetic tissue of a green plant; *of vegetation*, characteristic of moist habitats and with soft, fairly large leaves predominating; a leaf with an area within the approximate range 20–180 cm^2.

microgametophyte: a plant body or cell lineage, formed by vegetative growth of the microspore, that produces the male gametes of a heterosporous plant.

microphyll: small leaf.

micropyle: a small canal through the integument(s) of an ovule, persisting as a pore in the seed coat.

microsporangium: the smaller of the two kinds of sporangia produced in the sexual life cycle of a heterosporous plant.

microspore: the smaller of the two kinds of spores produced in the sexual life cycle of a heterosporous plant, giving rise to the male gametophyte.

microsporophyll: a specialised leaf upon (or in the axil of) which one or more microsporangia are borne.

midrib: the central, and usually the most prominent, vein of a leaf or leaf-like organ.

monadelphous: *of stamens*, united by their filaments into one bundle.

moniliform: cylindrical but constricted at regular intervals like a string of beads.

monocarpic: flowering and fruiting only once during its life span.

monochasium: a cymose inflorescence with the branches arising singly. pl. **monochasia**. cf. **dichasium**.

monochasial cyme: an inflorescence composed of monochasia. Fig. 131F.

monochlamydeous: *of a flower*, having only one whorl of perianth parts.

monoclinous: having male and female reproductive organs in the same flower.

monocotyledon: a flowering plant whose embryo has only one cotyledon (seed leaf). cf. **dicotyledon**.

monoecious: having the male and female reproductive structures in separate flowers but on the same plant. cf. **dioecious**.

monophyletic: derived from a single ancestral line. cf. **polyphyletic**.

monopodial: *of growth*, with a persistent terminal growing point producing many lateral organs successively; *of a stem*, growing in the above manner. cf. **sympodial**.

monotypic: containing only one taxon of the next lower rank (e.g. applied to a family containing only one genus). cf. **polytypic**.

morphocline: a graded series of character states of an homologous character.

morphology: the form and structure of an organism or part of an organism; the study of form and structure.

motile: actively moving; self-propelled.

mucilage: slimy material exuded by certain plants or plant organs. adj. **mucilaginous**. Fig. 139C.

mucous: slimy.

mucro: a sharp, abrupt terminal point. adj. **mucronate**. Fig. 126BB.

mucronulate: with a very small mucro; diminutive of mucronate.

multiplanar: *of divided leaves*, with the lobes held in several to many planes.

muricate: rough on the surface; covered with short, hard tubercles or hard outgrowths of the epidermis. Fig. 134J.

muriculate: rough with minute, short, hard points.

muticous: pointless, blunt, awnless.

mycorrhiza: a symbiotic union between a fungus and a plant root.

naked: *of sporangia*, not covered by an indusium; *of seeds*, exposed on the surface of a sporophyll (not enclosed within an ovary); *of flowers*, without perianth; *of protoplasts or gametes*, not bounded by a cell wall.

naturalised: introduced and reproducing itself without human assistance. cf. **adventive**, **introduced**.

navicular: boat-shaped.

nectary: a gland that secretes nectar. adj. **nectariferous**.

neotype: a specimen or illustration selected to serve in place of a holotype, where all of the material on which the name was originally based is missing or destroyed. cf. **lectotype**.

nerve: a vein.

nest-fronds: specialised, shield-like, basal fronds in some ferns (e.g *Platycerium)*which accumulate leaf-litter.

neuter: sterile (e.g. of flowers in which neither the androecium nor the gynoecium is functional in reproduction).

nocturnal: *of flowers*, opening only at night.

node: the level (transverse plane) of a stem at which one or more leaves arise.

nomen conservandum: a name of a family, genus or species that has been formally accepted under the *International Code for Botanical Nomenclature* as the correct name contrary to the usual principles of botanical nomenclature; abbrev. *nom. cons*.

nomen illegitimum: a name which, at the time of its publication, was superfluous (because it included the type of an earlier name which should have been adopted) or had already been applied to another plant; abbrev. *nom. illeg*.

nomen nudum: a name published without a diagnosis or description of the entity to which it was applied, and without reference to either; abbrev. *nom. nud*.

nomen rejiciendum: a name rejected in favour of a 'nomen conservandum'; abbrev. *nom. rej*.

nucellus: the central tissue of an ovule, within which the megaspore mother cell is formed.

nut: a hard, dry, indehiscent fruit formed from two or more carpels but containing only one seed.

obconical: cone-shaped but attached at the narrower end.

obcordate: *of a leaf blade*, broad and notched at the tip; heart-shaped but attached at the pointed end. Fig. 126GG.

oblanceolate: similar in shape to lanceolate but attached at the narrower end.

obligate: *of parasites*, unable to survive without the host. cf. **facultative**.

oblique: *of a leaf or leaflet*, larger on one side of the midrib than on the other, i.e. asymmetrical. Fig. 126U.

obloid: (a three-dimensional shape) with short, parallel sides and rounded ends, as if composed of two hemispheres linked together by a short cylinder.

oblong: having the length greater than the width but not many times greater, and the sides parallel. Fig. 126E.

obovate: similar in shape to ovate but attached at the narrower end. Fig. 126J.

obsolescent: non-functional but not reduced to a rudiment.

obsolete: reduced to a rudiment, or completely lacking. cf. **rudimentary**, **vestigial**.

obtrullate: a 2-dimensional shape resembling a trowel blade with the broadest axis above the middle and a length : breadth ratio between 3 : 2 and 2 : 1.

obtuse: blunt or rounded at the apex, the converging edges separated by an angle greater than 90°. Fig. 126DD.

ochrea: a sheath, formed from two stipules, encircling the node in Polygonaceae. Fig. 129B.

ontogeny: the development of a single organism, i.e. the sequence of stages through which it passes during its lifetime.

operculum: a lid or cover; the upper part of an organ, becoming detached or partially detached at maturity by abscission of transverse dehiscence; *in Eucalyptus*, a cap covering the bud and formed by fusion or cohesion of perianth parts. adj. **operculate**. Fig. 133L.

opposite: *of leaves,* borne at the same level but on opposite sides of the stem; *of floral parts*, on the same radius. cf. **alternate**. Fig. 130M.

orbicular: circular or nearly so. Fig. 126K.

order: a taxonomic grouping of families believed to be closely related (sometimes a single family with no apparent close relatives); the major taxonomic rank between family and class.

orthotropous: *of an ovule*, erect so that the micropyle points away from the placenta. Fig. 136K.

ostiole: an opening or pore, e.g. at the apex of a fig.

ovary: the basal portion of a carpel or group of fused carpels, enclosing the ovule(s).

ovate: a two dimensional shape, like a section through the long axis of an egg, and attached by the wider end. cf. **ovoid**. Fig. 126I.

ovoid: egg-shaped (in three dimensions). cf. **ovate**.

ovulate: with ovules.

ovule: a structure in a seed plant within which one or more megaspores are formed and which develops into a seed after fertilisation. Fig. 136E–M.

ovuliferous: bearing ovules (e.g. applied to scales in a megasporangiate cone in gymnosperms).

ovulode: sterile structures on the placenta.

palea: *in a grass floret*, the upper one of the two bracts enclosing a flower.

palmate: *of a leaf*, divided into several leaflets which arise at the same point. Figs 127I, 128J.

palmatifid: *of a leaf*, deeply (but not completely) divided into several lobes which arise (almost) at the same level. cf. **pinnatifid**, **palmate**, **palmatisect**. Fig. 127G.

palmatinerved: *of leaves*, palmately nerved, i.e. with the (main) nerves radiating from one basal point.

palmatisect: a condition intermediate between palmate and palmatifid, with the green tissue of the lamina completely divided into several segments, but the segments not fully separated at the base. Fig. 127H.

palynology: the scientific study of pollen.

pandurate: fiddle-shaped.

panicle: a compound raceme; an indeterminate inflorescence in which the flowers are borne on branches of the main axis or on further branches of these. Fig. 131D.

paniculate: indeterminate and much branched.

pantoporate: *of a pollen grain*, with rounded apertures all over the surface.

papilla: a small, elongated protuberance on the surface of an organ, usually an extension of one epidermal cell. adj. **papillose**. Figs 134N, 137I.

pappus: a tuft (or ring) of hairs or scales borne above the ovary and outside the corolla in Asteraceae and possibly representing the calyx; a tuft of hairs on a fruit. Fig. 138L.

parapatric: *of distributions of two taxa or populations*, having non-overlapping but contiguous ranges.

paraphyletic: a group of taxa derived from a single ancestral taxon, but which does not contain all the descendants of the most recent common ancestor.

paraphyses: sterile filaments in the fruiting bodies of non-vascular plants.

parasite: an organism living on or in a different organism and deriving nourishment from it. cf. **saprophyte**, **epiphyte**.

paratype: a specimen or illustration, other than the holotype, isotype or one of the syntypes, that was cited with the original publication of a name.

parenchyma: plant tissue consisting of mature, living cells that are relatively unspecialised in function.

parietal: attached to the margins of a structure; *of placentation*, having the ovules attached to placentas on the wall of the ovary. Fig. 136G.

paripinnate: having an even number of pinnae by virtue of having a pair in the terminal position. cf. **imparipinnate**. Fig. 127L.

-partite: divided, almost to the base, into segments (commonly applied to a style).

pectinate: comb-like.

pedate: *of a palmate or palmately-lobed leaf*, having the lateral segments divided again.

pedicel: the stalk of a flower. adj. **pedicellate**.

peduncle: the stalk of an inflorescence; *in ferns*, the stalk of a sporocarp. adj. **pedunculate**.

pellucid: transparent.

peloric: actinomorphic, *of a flower which, from its taxonomic context, would be expected to be zygomorphic*, e.g. in Orchidaceae.

peltate: *of a leaf*, having the stalk attached to the lower surface of the blade, not to the margin (also applied, in the same sense, to other stalked structures). Figs 126K, 139L.

pendulous: drooping; *of ovules*, attached at the top of the ovary and hanging downwards from an apical placenta.

penicillate: pencil-shaped; tufted like an artist's brush.

penninerved (= **penniveined**): having conspicuous lateral veins divergent from the midrib and lying approximately parallel to each other.

pentamerous: *of a flower*, having five parts in each floral whorl (not necessarily including the gynoecium).

pepo: *literally*, a pumpkin (Latin); a fruit with firm skin, pulpy interior, many seeds and a single locule.

perennate: maintain a dormant, vegetative state throughout non-growing seasons.

perennial: a plant whose life span extends over more than two growing seasons.

perfoliate: *of a sessile leaf or bract*, having its base completely wrapped around the stem. Fig. 128F.

perianth: the calyx and corolla of a flower, especially where the two are similar.

pericarp: the wall of a fruit, developed from the ovary wall.

perigynous: *of perianth segments and stamens*, arising from a cup or tube (hypanthium) that is free from the ovary but extending above its base. cf. **hypogynous**, **epigynous**. Fig. 135B.

perisperm: nutritive tissue in an angiospermous seed, formed from the nucellus. cf. **endosperm**.

persistent: remaining attached to the plant beyond the expected time of falling (e.g. of sepals not falling after flowering).

petal: a member of the inner whorl of non-fertile parts surrounding the fertile organs of a flower, usually soft and coloured conspicuously.

petaloid: like a petal; soft in texture and coloured conspicuously.

petiole: the stalk of a leaf. Fig. 128A.

petiolule: the stalk of a leaflet.

phalange: a bundle comprising several structures fused together; a group of connate carpels, e.g. in Pandanaceae.

phanerogam: (literally) a plant with conspicuous reproductive parts; a plant reproducing by seeds. cf. **cryptogam**.

phenotype: the physical characteristics of an organism; the outward expression of characteristics conferred on an organism by its genotype. cf. **genotype**.

phloem: the tissue in the conducting system of a plant through which metabolites (products of chemical reactions in the plant) are transported.

phyllichnium: *in Casuarinaceae*, the ridge of a branchlet segment; pl. **phyllichnia**.

phylloclade: a very leaf-like, photosynthetic stem of a plant whose true leaves are much reduced. cf. **cladophyll**.

phyllode: a leaf whose blade is much reduced or absent, and whose petiole and rachis have assumed the functions of the whole leaf. cf. **cladode**.

phyllotaxy: the arrangement of leaves on a stem (when spiral, often expressed quantitatively as the fraction of the circumference of the stem that separates two successive leaves).

phylogeny: the evolutionary development of a plant group, i.e. its derivation from its ancestors and the relationship among its members. adj. **phylogenetic**.

phylum: an alternate name for division, the major taxonomic rank below kingdom.

pilose: hairy, the hairs soft and clearly separated but not sparse. Fig. 137J.

pinna: a primary segment of the blade of a compound leaf. pl. **pinnae**.

pinnate: divided into pinnae; once-compound. cf. **bipinnate**, **tripinnate**. Figs 127L–M, 128I.

pinnatifid: cut deeply (but not to midrib) into lobes that are spaced out along the axis (of the leaf). cf. **palmatifid**. Fig. 127B.

pinnatipartite: *of leaves*, pinnatifid, where the lobes pass beyond the middle (or are within the middle third) and the parenchyma is not interrupted.

pinnatisect: dissected down to the midrib but having the segments confluent with it. Fig. 127C.

pinnule: a leaflet of a bipinnate leaf.

pistil: a free carpel or a group of fused carpels.

pistillode: a sterile pistil, often rudimentary.

pith: the central region of a stem, inside the vascular cylinder.

placenta: a region, within an ovary, to which ovules are attached.

placentation: the arrangement of placentas, and hence of ovules, within an ovary. Fig. 136E–J.

plesiomorphic: *of a character*, ancestral or primitive.

plicate: folded back and forth longitudinally like a fan. Fig. 130E.

plietesial: monocarpic but living for several years before flowering.

plumose: like a feather; with fine hairs branching from a central axis. Fig. 139J.

plumule: the portion of an embryo that gives rise to the shoot system (as distinct from the root system) of a plant. cf. **radicle**.

pneumatophore: an air-vessel; an organ containing aerenchyma; *in particular*, a root of a mangrove plant, growing above the substratum.

pod: a leguminous fruit. Fig. 134A.

pollen: the microspores of seed plants; the powdery mass of microspores shed from anthers.

pollen-grain: see grain.

pollen presenter: *of many Proteaceae*, a structural modification, usually a swelling, of the style around or below the stigma which enables pollen, shed in the bud, to be retained.

pollen-sac: see sac.

pollination: the transfer of pollen from the male organ, where it is formed, to the receptive region of a female organ, e.g. from anther to stigma.

pollinarium: the complex structure found in flowers of Asclepiadaceae where the pollen masses of the two adjacent anther-lobes (thecae) are united for dispersal as a unit. The pollinarium consists of two pollinia, two caudicles and a corpusculum. plur. **pollinaria**.

pollinium: a cohering mass of pollen grains from one anther-lobe (theca), transferred as a unit in pollination. pl. **pollinia**.

polygamodioecious: with bisexual and male flowers on some plants, and bisexual and female flowers on others.

polygamomonoecious: with bisexual flowers and unisexual flowers of both sexes on the same plant.

polygamous: having bisexual and unisexual flowers on the same or different plants.

polymorphic: having more than two distinct morphological variants.

polypetalous: with free petals. cf. **gamopetalous**.

polyphyletic: composed of members that originated, independently, from more than one evolutionary line. cf. **monophyletic**.

polyploid: having more than two of the basic sets of chromosomes in the nucleus.

polytypic: containing more than one taxon of the next lower rank. cf. **monotypic**.

pome: a fleshy (false) fruit, formed from an inferior ovary, in which the receptacle or hypanthium has enlarged to enclose the true fruit.

porate: *of a pollen grain*, with rounded apertures only. cf. **colporate**, **colpate**.

poricidal: *of anthers or capsules*, opening by pores. Fig. 133M.

porrect: *of a trichome*, having branches spreading more or less horizontally from the top of an erect stalk. Fig. 139K.

posterior: *of floral parts*, on the side of the flower nearest to the axis. cf. **anterior**.

powdery: covered with fine, powdery particles.

praemorse: appearing bitten off at the end.

prickle: a hard, pointed outgrowth from the surface of a plant, involving several layers of cells but not containing a vein. Fig. 139E.

process: *as part of a plant*, a projecting outgrowth or appendage.

procumbent: trailing or spreading along the ground but not rooting at the nodes.

proliferous: able to reproduce vegetatively from the shoot system, e.g. by stems rooting at the nodes (as in *Conostylis)*; producing plantlets on leaves or fronds (*Pteris*) or in the inflorescence (*Isolepis).*

propagule: a structure with the capacity to give rise to a new plant, e.g. a seed, a spore, part of the vegetative body capable of independent growth if detached from the parent.

prophyll: a leaf formed at the base of a shoot, usually smaller than those formed subsequently.

prostrate: lying flat on the ground.

protandrous: having the male sex organs maturing before the female; *of a flower*, shedding the pollen before the stigma is receptive. cf. **protogynous**.

prothallus: a gametophyte body, especially in bryophytes, ferns and related plants.

protogynous: having the female sex organs maturing before the male; *of a flower*, shedding the pollen after the stigma has ceased to be receptive. cf. **protandrous**.

proximal: near to the point of origin or attachment. cf. **distal**.

pruinose: having a whitish, waxy, powdery bloom on the surface.

pseudanthium: a compact inflorescence of several to many small flowers which simulates a single flower.

pseudo-: false; apparent but not genuine.

pseudostipel: extensions of dorsal ridges on the petioles (e.g. of *Neptunia*.

puberulous: covered with minute, soft, erect hairs. Fig. 137K.

pubescent: covered with short, soft, erect hairs. Fig. 137L.

pulverulent: as though dusted over with powder.

pulvinate: cushion- or pad-shaped, resembling a pulvinus.

pulvinus: a swelling at the base of the stalk of a leaf or leaflet, often glandular or responsive to touch. Fig. 130J.

punctate: marked with dots.

puncticulate: minutely dotted.

pungent: ending in a stiff, sharp point; having an acrid taste or smell.

pustulate: covered with small pustule- or blister-like elevations.

pyrene: the 'stone' (endocarp plus seed) of a succulent fruit. cf. **berry**, **drupe**.

quincuncial: *of the arrangement of corolla lobes in a bud*, a variant of imbricate aestivation. Fig. 136B.

raceme: an indeterminate inflorescence in which a main axis produces a series of flowers on lateral stalks, the oldest at the base and the youngest at the top. adj. **racemose**. Fig. 131C.

racemule: secondary raceme in a compound raceme or umbellate inflorescence.

rachilla: (= **rhachilla**) *of palms and woody monocotyledons*, the lateral or secondary branches of the inflorescence; *of a grass spikelet*, the axis above the glumes.

rachis: (= **rhachis**) the axis of an inflorescence or a pinnate leaf; pl. **rachises**. **secondary rachis:** the axis of a pinna in a bipinnate leaf.

radical: *of leaves*, clustered at the base of the stem.

radicle: the portion of an embryo that gives rise to the root system of a plant. cf. **plumule**.

ramiflorous: *of flowers and fruits*, borne below the current leaves on recently formed woody branches. cf. **cauliflorous**.

ramuliflorous: flowering on branchlets.

raphe: the part of the stalk of an anatropous ovule that is fused along the side of the ovule.

raphides: needle-like crystals that occur in bundles in the vacuoles of some plant cells.

ray: *in woody stems*, a radial band of cells traversing the conducting elements; *of a compound umbel*, one of the first (lower) series of branches of the inflorescence axis.

ray floret: a zygomorphic flower in Asteraceae.

receptacle: the axis of a flower (= **torus**); *in ferns*, an axis on which sporangia arise.

reclinate: bent back from the axis, attachment, or point of reference, but not curving. cf. **declinate**.

recurved: curved or curled downwards or backwards.

reflexed: bent sharply downwards or backwards.

regular: see actinomorphic.

reniform: kidney-shaped. Fig. 126O.

replum: a longitudinal partition in an ovary, formed between parietal placentas.

resupinate: twisted through 180°, e.g. as with the ovary of most Orchidaceae.

reticulate: forming a network. Fig. 134E.

retinaculum: a hook-like structure to which another structure is tethered; *in Orchidaceae and Asclepiadaceae*, the structure to which pollen masses are attached; *in Acanthaceae*, the persistent stalk of an ovule.

retrorse: bent, and pointing away from the apex. cf. **antrorse**.

retuse: with a very blunt and slightly notched apex. Fig. 126EE.

revolute: rolled downwards or backwards; *of a leaf lamina*, with the margins rolled towards the abaxial surface. cf. **involute**. Fig. 130B.

rhachilla: see rachilla.

rhachis: see rachis.

rhipidium: a compound cyme with the lateral branches developed alternately on one side and then the other.

rhizoid: a thread-like, unicellular absorbing structure occurring, in the vascular plants, in gametophytes of ferns and some related plants.

rhizome: an underground stem, usually growing horizontally. Fig. 125G.

rhizophore: *in Selaginella*, a leafless stem that produces roots.

rhomboid: quadrangular, with the lateral angles obtuse. Fig. 126M.

root: unit of the axial system of a plant which is usually underground, does not bear leaves, tends to grow downwards and is typically derived from the radicle of the embryo. cf. **adventitious.**

rootstock: a short, erect, swollen structure at the junction of the root and shoot systems of a plant (loosely: the root system).

rostellum: *in Orchidaceae*, a beak-like upward extension of the stigma.

rostrate: beaked.

rosulate: clustered into a rosette, e.g. of basal leaves of some annual and biennial forbs.

rotate: circular and flattened, e.g. of a corolla with a very short tube and spreading lobes.

rudimentary: poorly developed and not functional. cf. **vestigial**, **obsolete**.

rugose: deeply wrinkled.

rugulose: covered with minute wrinkles.

ruminate: mottled in appearance, e.g. of bark, or of the food reserves in a seed.

runcinate: deeply lobed and with the lobes slanted away from the apex. Fig. 127F.

runner: a slender, prostrate or trailing stem which produces roots and sometimes erect shoots at its nodes. cf. **stolon**.

sac: a pouch or cavity; **pollen-sac:** a cavity, in an anther, in which pollen is formed; **embryo-sac:** a large, multi-nucleate cell in which an egg nucleus is formed and fertilised, and in which an embryo begins to develop.

saccate: pouched.

sagittate: shaped like an arrow-head. Fig. 126S.

salverform: *of a sympetalous corolla*, salver-shaped, i.e. with a slender tube and abruptly expanded flat, rotate limb (like the corolla of *Primula*).

samara: a dry, indehiscent fruit with its wall expanded into a wing.

saprophyte: an organism deriving its nourishment from dead organic matter and usually lacking chlorophyll. cf. **epiphyte**, **parasite**.

scaberulous: slightly or minutely rough to the touch, minutely scabrous.

scabridulous: slightly rough; diminutive of scabrous.

scabrous (= **scabrid**)**:** rough to the touch. Fig. 138A.

scalariform: having a ladder-like pattern.

scale: a reduced or rudimentary leaf, e.g. surrounding a dormant bud; a thin flap of tissue of epidermal origin, e.g. at the base of a stamen in Simaroubaceae; a thin scarious trichome which is flattened and variously shaped. Fig. 139L.

scandent: climbing.

scape: the stem-like, flowering stalk of a plant with radical or rosulate leaves.

scarious: dry and membranous.

schizocarp: a dry fruit formed from more than one carpel but breaking apart into 1-carpel units when ripe. cf. **mericarp**.

sclerenchyma: mechanical tissue with heavily thickened cell walls.

sclereid: a cell (usually elongated) with a strongly lignified wall.

scleromorph: a plant whose leaves (or stems, if leafless) are hard in texture, usually having thick cuticle and containing many fibres. cf. **xeromorph**.

sclerophyllous: with leaves stiffened by sclerenchyma.

scorpioid: *of a cymose inflorescence*, branching alternately on one side and then the other, with the main axis coiled like the tail of a scorpion. cf. **helicoid**.

scribble: irregular lines on the bark of some eucalypts, being the old tunnels burrowed by moth larvae between bark layers and exposed when the outer layer falls.

secund: with all the parts grouped on one side or turned to one side (applied especially to the grouping of flowers in an inflorescence or stamens in a flower).

seed: a propagating organ formed in the sexual reproductive cycle of gymnosperms and angiosperms, consisting of a protective coat enclosing an embryo and food reserves. Fig. 134E–N.

segment: a part or sub-division of a divided organ; one of a group of similar organs named collectively, e.g. one petal = a segment of a corolla.

semicraspedodromus: pinnate venation in which the secondary veins branch just inside the margin, one of the branches terminating at the margin, the other joining the superadjacent secondary vein.

sepal: a member of the (usually green) outer whorl of non-fertile parts surrounding the fertile organs of a flower.

sepaloid: looking like sepals, e.g. *of bracts*, usually green and arranged in a ring beneath a flower.

septate: divided internally by partitions.

septicidal: *of the dehiscence of a fruit*, along lines coinciding with the partitions between loculi. cf. **loculicidal**. Fig. 134C.

septifragal: *of the dehiscence of a fruit*, the valves or backs of the carpels breaking away leaving the septa intact.

septum: a partition. pl. **septa**.

seriate: in rows or whorls.

sericeous: silky; covered with silky hairs.

serrate: toothed, with asymmetrical teeth pointing forward. Fig. 127P.

serrulate: finely serrate. Fig. 127Q.

sessile: without a stalk (when applied to a stigma, indicates that the style is absent, the stigma being 'sessile' on the ovary). Fig. 128B.

seta: a bristle or stiff hair; terminal seta: an appendage to the tip of an organ, e.g. to the primary rachis of a bipinnate leaf in *Acacia*. adj. **setaceous**.

setiferous: bearing setae.

setose: covered with bristles.

setulose: covered with fine bristles; resembling a fine bristle.

sheath: the lower portion of of a grass leaf, clasping the stem; one of the wing-like extensions to the margins of the petiole which wrap around and enclose the stem; **closed sheath:** one in which the wings are fused to form a cylinder; **open sheath:** one with a slit on the side opposite to the lamina. Fig. 128D, E.

shrub: a woody plant less than 5 metres high, either without a distinct main axis, or with branches persisting on the main axis almost to its base.

sigmoid: doubly curved in opposite directions like the letter S.

siliceous: containing silica.

silicula: a short siliqua, not more than twice as long as its width.

siliqua: a dry, dehiscent fruit formed from a superior ovary of two carpels, with two parietal placentas and divided into two loculi by a false septum between the placentas.

silky: densely covered with fine, soft, straight, appressed hairs, with a lustrous sheen and satin-like to the touch. Fig. 138B.

simple: undivided; *of a leaf*, not divided into leaflets; *of a hair or an inflorescence*, not branched.

sinistrorse: turned towards the left. cf. **dextrorse**.

sinuate: with deep, wave-like depressions along the margin. cf. **undulate**. Fig. 127V.

sinus: a notch or depression in the margin of an organ.

smooth: of surfaces, even, without roughness or indumentum.

solitary: *of flowers*, borne singly, not grouped in an inflorescence.

sorus: *in ferns*, a discrete group of sporangia. pl. **sori**.

spadix: a spicate inflorescence with a stout, often succulent axis. Fig. 133H.

spathaceous: like a spathe; with a spathe.

spathe: a large bract ensheathing an inflorescence. Fig. 133H.

spathella: a closed membranous sac which envelopes the immature flower in some Podostemaceae, rupturing irregularly as the pedicel elongates at anthesis.

spathulate (= **spatulate**)**:** spoon-shaped; broad at the tip and narrowed towards the base. Fig. 126P.

species: a taxon comprising one or more populations of individuals capable of interbreeding to produce fertile offspring.

spike: an unbranched, indeterminate inflorescence in which the flowers are without stalks. adj. **spicate**. Fig. 131B.

spikelet: a unit of the inflorescence in grasses, sedges and some other monocotyledons, consisting of one to many flowers and associated glumes. Fig. 131A.

spine: a stiff, sharp-pointed structure, formed by modification of a plant organ, e.g. a lateral branch or a stipule. adj. **spinulose**. Figs 134I, 139F.

spinescent: ending in a spine; modified to form a spine.

spinose: bearing spines.

spiral: *of leaves or floral organs*, borne at different levels on the axis, in an ascending spiral. cf. **cyclic**. Fig. 130K.

sporangiate: bearing spores (or pollen).

sporangiophore: the stalk of a sporangium; *in Botrychium*, the branched axis bearing sporangia.

sporangium: a structure within which spores are formed. pl. **sporangia**.

spore: a simple propagule, produced either sexually or asexually, and consisting of one or a few cells.

sporocarp: a fruiting body containing sporangia.

sporogenous: *of cells or tissues*, spore-generating.

sporophyll: a specialised leaf-like organ on which one or more sporangia are borne.

sporophyte: a plant, or phase of a life cycle, that bears the spores formed during the sexual reproductive cycle.

spur: a tubular pouch at the base of a perianth part, often containing nectar.

stamen: one of the male organs of a flower, consisting typically of a stalk (filament) and a pollen-bearing portion (anther). adj. **staminate**. Fig. 132J–M.

staminal corona: fleshy outgrowths of tissue, attached dorsally to the staminal column at the base of the filaments or on the backs of the anthers. cf. **gynostegial corona**.

staminode: a sterile stamen, often rudimentary, sometimes modified (e.g. petaloid).

staminophore: a band of tissue around the apex of the hypanthium in a eucalypt flower, on which the stamens are inserted.

standard: (= **vexillum**)**:** the posterior petal in the flower in Fabaceae and Caesalpiniaceae.

stellate: star-shaped; consisting of star-shaped cells; a branched trichome with six or more branches radiating from a single point. Fig. 139K.

stem: the main axis or a branch of the main axial system of a plant, developed from the plumule of the embryo and typically bearing leaves.

stigma: the pollen-receptive surface of a carpel or group of fused carpels, usually sticky.

stinging trichome: a hollow trichome seated on a gland which, when broken, secretes an irritating fluid.

stipe: a small stalk; *in ferns*, the petiole of a frond.

stipel (= stipella): stipule-like appendage at the base of a leaflet (in unifoliolate leaves, inserted on the petiole, not on the stem). pl. **stipellae**. adj. **stipellate**. Fig. 129J.

stipitate: stalked; borne on a stipe; *of an ovary*, borne on a gynophore.

stipule: one of a pair of appendages at the bases of leaves in many dicotyledons. Fig. 129A–I.

stolon: a prostrate or trailing stem that produces roots at the nodes. cf. **runner**. Fig. 125F.

stoloniferous: having stolons; trailing over the soil surface and rooting at the nodes.

stoma: a pore; a pore in the epidermis of a leaf or other aerial organ, providing for gaseous exchange between the tissues and the atmosphere. pl. **stomata**.

stomium: a region of dehiscence, e.g. of an anther in flowering plants. pl. **stomia**.

stone cell: a ±isodiametric sclereid.

stramineous: straw coloured.

striate: striped with parallel longitudinal lines or ridges. Fig. 134H.

strigose: with sharp, stiff hairs which are appressed to the surface. Fig. 138C.

strigulose: minutely strigose.

strobilus: a 'cone' consisting of sporophylls borne close together on an axis.

strophiole: see caruncle.

struma: a cushion-like swelling, e.g. at the apex of staminal filaments in *Dianella*.

style: an elongated part of a carpel, or group of fused carpels, between the ovary and the stigma.

stylopodium: a disc-like enlargement of the base of the style.

subulate: narrow and tapering gradually to a fine point. Fig. 126A.

sulcate: grooved; furrowed.

superior: *of an ovary*, borne above the level of attachment of the other floral parts, or above the base of a cup (hypanthium) that is free from the ovary and bears the perianth segments and stamens. cf. **inferior**. Fig. 135A–C.

suture: a line of junction between two fused organs; a line of dehiscence.

syconium: a multiple fruit with a hollow centre, e.g. in *Ficus* (fig). Fig. 133I.

sympatric: *of two or more species*, having coincident or overlapping ranges of distribution. cf. **allopatric**.

sympetalous: (= **gamopetalous**)**:** with the petals united by their margins, at least at the base. cf. **polypetalous**.

sympodial: *of growth*, without a single, persistent growing point; changing direction by frequent replacement of the growing apex by a lateral growing point below it; *of a stem*, growing in the above manner. cf. **monopodial**.

synandrium: an androecium with the anthers of the stamens cohering. cf. **syngenesious**.

synangium: a group of fruits fused into a single structure; *in ferns*, a group of fused sporangia.

synapomorphic: the common possession by two taxa of a derived, homologous character.

syncarp: a structure consisting of several united fruits, usually fleshy. cf. **aggregate fruit**.

syncarpous: *of a flower*, having two or more carpels, all fused together.

syngenesious: *of the stamens of one flower*, fused together by the anthers e.g. in Asteraceae. cf. **monadelphous**.

syntepalum: *in some Musaceae*, a unilaterally split tube formed by the coherence of 3 sepals and 2 petals.

syntype: one of two or more specimens cited by the author at the time of publication of a name if no holotype was designated; any one of two or more specimens simultaneously designated as types.

tannin: a complex, aromatic compound occurring in the bark of many shrubs and trees.

tanniniferous: producing tannins.

taproot: the main, descending root of a plant that has a single, dominant root axis.

taxon: a group or category, at any level, in a system for classifying plants or animals. pl. **taxa**.

tendril: a slender climbing organ formed by modification of a part of a plant, e.g. a stem, a leaf or leaflet, a stipule.

tenuiexinous: *of a pollen grain*, with a thin exine.

tepal: a perianth segment in a flower in which all the perianth segments are similar in appearance.

terete: cylindrical or nearly so; circular in cross-section. Fig. 130F.

terminal: at the apex or distal end. Fig. 133A.

ternate: in groups of three; *of leaves*, arranged in whorls of three; *of a single leaf*, having the leaflets arranged in groups of three. Fig. 127K.

ternatifid: *of leaves*, deeply cut into three lobes.

terrestrial: of or on the ground; *of the habitat of a plant*, on land as opposed to in water, or on the ground as opposed to on another plant.

testa: a seed coat.

tetrad: a group of four; four pollen grains remaining fused together at maturity, e.g. in Ericaceae, Epacridaceae.

tetradynamous: *of an androecium*, consisting of four stamens of the same length and two of a different length.

tetramerous: *of a flower*, having four segments in each perianth whorl, and usually four in each whorl of stamens also.

thallus: the vegetative body of a plant that is not differentiated into organs such as stems and leaves, e.g. the gametophytes of ferns, and Lemnaceae.

thigmotaxis: a response, by movement or growth, to a mechanical stimulus, e.g. the leaves of 'Sensitive Plant' (*Mimosa*), the leaf hairs of *Drosera*, or the tendrils of many climbing plants. adj. **thigmotactic**.

thorn: a modified plant organ, especially a stem, that is stiffened and terminates in a pungent point.

throat: *of a corolla tube*, the top, where the tube joins the lobes.

thyrse: a branched inflorescence in which the main axis is indeterminate and the lateral branches determinate in their growth. Fig. 131 I.

tomentellous: minutely tomentose.

tomentum: a covering of dense, matted, woolly hairs. adj. **tomentose**. Fig. 138D.

torus: see receptacle.

trabecula: a transverse partition dividing or partly dividing a cavity.

translator: applied to parts of a pollinarium, comprising the central part or corpusculum, and the arm-like structures or caudicles uniting the corpusculum with the pollinia.

trapeziform: having four straight unequal sides.

tree: a woody plant at least 5 metres high, with a main axis the lower part of which is usually unbranched.

trichome: an epidermal outgrowth, e.g. a hair (branched or unbranched), a papilla. Fig. 139.

trichotomous: branching almost equally into three parts.

trifid: deeply divided into three parts.

trifoliate: having three leaves.

trifoliolate: *of a leaf*, having three leaflets. Fig. 127J.

trigonous: triangular in cross-section and obtusely-angled. cf. **triquetrous**.

trimerous: *of a flower*, having three segments in each perianth whorl and usually three in each whorl of stamens also.

tripartite: divided into three parts.

tripinnate: *of leaves*, thrice pinnately divided.

triplicate: folded three times.

triquetrous: triangular in cross-section and acutely-angled; with three distinct longitudinal ridges. cf. **trigonous**.

tristichous: arranged in three rows on a stem, each row in the same plane.

tristylous: heterostylous species having three style lengths (short, mid, long), the flowers of any one plant having styles of the same length.

trulliform: shaped like a bricklayer's trowel, i.e. angular-ovate, broadest below the middle, rhomboid with the two lower equal sides shorter than the upper.

truncate: with an abruptly transverse end, as if cut off. Fig. 126V.

tuber: a storage organ formed by swelling of an underground stem or the distal end of a root.

tubercle: a small wart-like outgrowth.

tuberculate: covered with tubercles. Fig. 134L.

tuberous: swollen; *of roots*, tuber-like.

tumid: swollen; inflated.

tunic: *of a bulb or corm*, the thin membranous or fibrous outer layers.

turbinate: top-shaped, obconical.

turgid: swollen due to high water content. cf. **flaccid**.

turion: an over-wintering vegetative bud or specialised short shoot with modified leaves, arising from the stem, often near ground level. Fig. 125D.

type: a designated representative (standard) for a plant name. cf. **isotype**, **holotype**, **neotype**, **syntype**.

umbel: a racemose inflorescence in which all the individual flower stalks arise in a cluster at the top of the peduncle and are of about equal length. Fig. 131J, K.

umbellule: secondary umbel in a compound umbellate inflorescence.

uncinate: terminating in a hooked point.

undulate: wavy, i.e. not flat. cf. **sinuate**. Figs 127W, 130D.

unifoliate: having one leaf.

unifoliolate: *of a leaf*, basically compound, but reduced to only one leaflet.

unilateral: *of stamens*, with anthers grouped on one side of the style.

unilocular: *of an ovary, anther or fruit*, having only one internal cavity.

unisexual: bearing only male or only female reproductive organs.

united: fused together.

urceolate: urn-shaped.

utricle: a small bladder; a membranous bladder-like sac enclosing an ovary or fruit.

valvate: *of sepals or petals in a bud*, meeting edge to edge, not overlapping. cf. **imbricate**. Fig. 136D.

valve: a portion of an organ that has fragmented; *of a capsule*, the teeth-like portions into which the dehiscing part of the pericarp splits at maturity. Fig. 132E.

vascular: specialised for conduction of fluids; vascular plants: plants containing specialised conducting tissues.

vein: a strand of vascular tissue. Figs 128H–L.

velamen: a water-retaining outer layer of the aerial roots of some epiphytes, especially orchids.

velvety: very densely covered with fine, short, soft, erect hairs. Fig. 138E.

velum: a membranous covering; a veil.

venation: the arrangement of veins in a leaf.

ventral: *of a lateral organ*, facing towards the subtending axis; *of a thallus*, facing towards the substratum. cf. **dorsal**.

vernation: the arrangement of unexpanded leaves in a bud. cf. **aestivation**.

vernicose: varnished.

verrucose: covered with wart-like outgrowths, warted.

verruculose: covered with closely spaced, minute wart-like outgrowths.

versatile: *of anthers*, swinging freely about the point of attachment to the filament, which is approximately central. cf. **basifixed**, **medifixed**.

verticil: a whorl or circular arrangement of similar parts around an axis.

verticillaster: a false whorl of opposed cymes. Fig. 131H.

verticillate: arranged in one or more whorls; a false whorl of flowers in a pair of opposite dense cymes, especially in Lamiaceae.

vesicle: a bladder-like sac or cavity filled with gas or liquid. Fig. 138F.

vessel: a capillary tube formed from a series of open-ended cells in the water-conducting tissue of a plant.

vestigial: reduced from the ancestral condition and no longer functional. cf. **obsolete**, **rudimentary**.

vexillum: (= **standard**).

villous: shaggy with long, weak hairs. cf. **hirsute**. Fig. 138G.

viscid: *of a surface*, sticky; coated with a thick, syrupy secretion.

viscidium: *of orchids*, a viscid part of the rostellum which is clearly defined and removed with the pollinia as a unit, serving to attach the pollinia to an insect or other pollination vector.

viscous: *of a liquid*, not pouring freely; having the consistency of syrup or honey.

viviparous: *of seeds or fruits*, germinating before being shed from the parent plant.

wallum: coastal vegetation on sandy acidic soils, in south-eastern Qld.

warty: covered with wart-like protuberances. Fig. 138H.

whorl: a ring of leaves, bracts or floral parts borne at the same level on an axis. Fig. 130N.

wing: a membranous expansion of a fruit or seed, which aids dispersal; a thin flange of tissue extended beyond the normal outline of a stem or petiole; a lateral petal of a flower in Fabaceae.

woolly: very densely covered with long, soft, more or less matted or intertwined trichomes, resembling sheep's wool. Fig. 138I.

xeromorph: a plant having structural features usually associated with plants of arid habitats (such as hard or succulent leaves) but not necessarily drought-tolerant. cf. **scleromorph**, **xerophyte**.

xerophyte: a drought-tolerant plant. cf. **xeromorph**.

xylem: the tissue, in a vascular plant, that conducts water and mineral salts from the roots to the leaves.

zygomorphic: *of a flower or calyx or corolla*, bilaterally symmetrical, symmetrical about one plane only, usually the plane that bisects the flower vertically along the longitudinal axis. cf. **actinomorphic**, **peloric**.

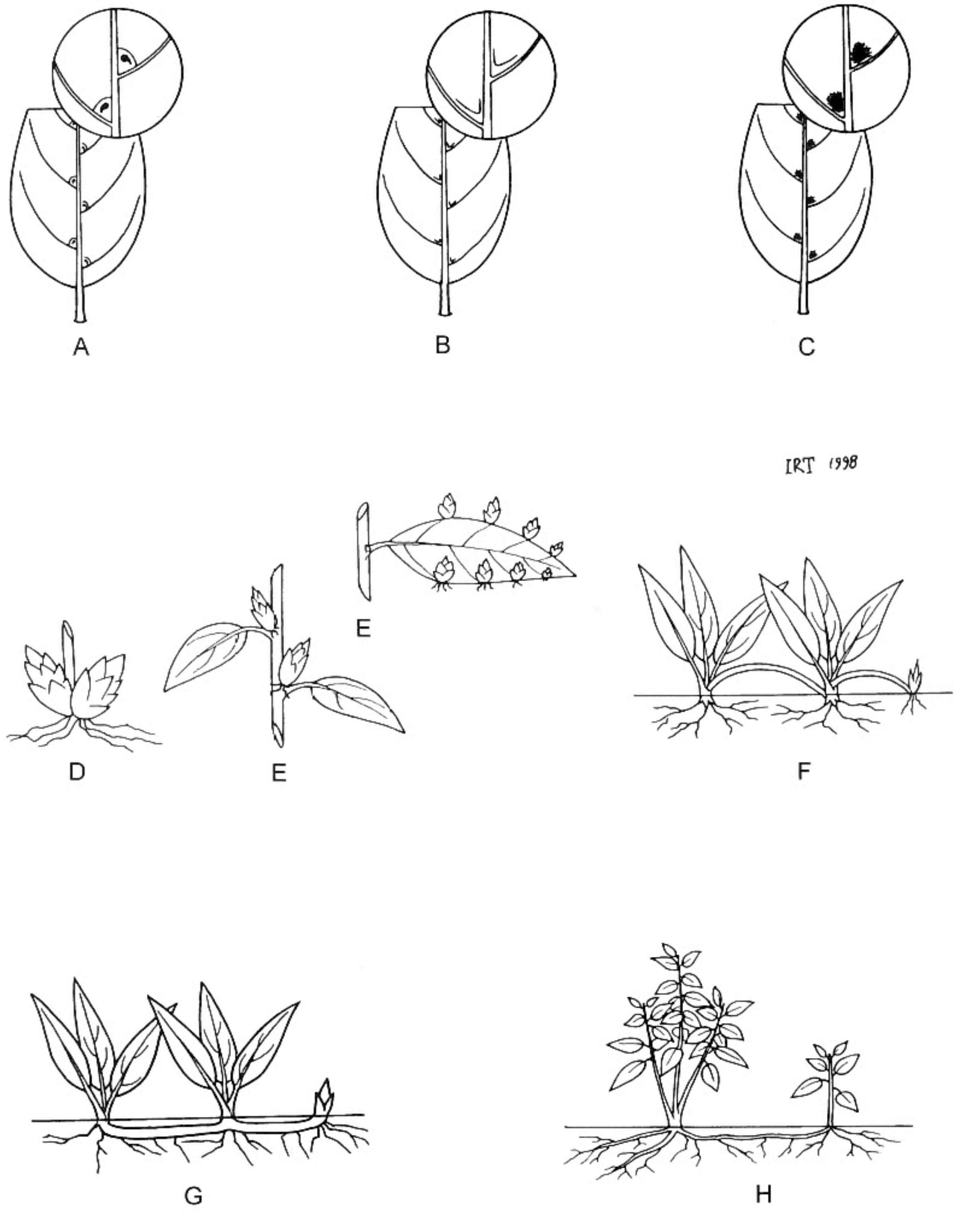

Figure 125. **A–C**, Domatia, **A**, pits; **B**, pockets; **C**, hair tufts. **D–H**, Perennating/vegetative reproduction. **D**, turion; **E**, bulbils; **F**, stolons; **G**, rhizome; **H**, root suckers. Drawn by I.Telford.

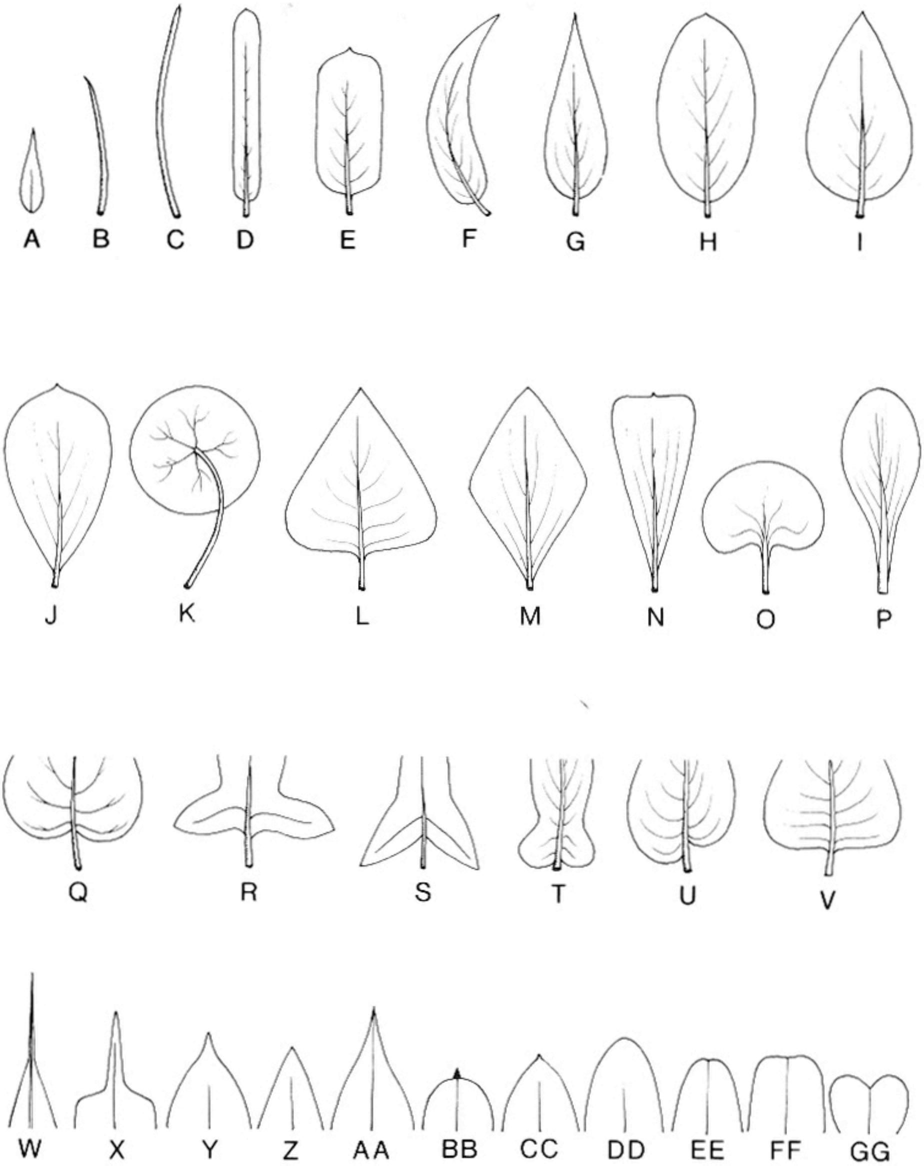

Figure 126. A–P, Leaf shapes, **A**, subulate; **B**, acicular; **C**, filiform; **D**, linear; **E**, oblong; **F**, falcate; **G**, lanceolate; **H**, elliptic; **I**, ovate; **J**, obovate; **K**, orbicular and peltate; **L**, deltoid; **M**, rhomboid; **N**, cuneate; **O**, reniform; **P**, spathulate. **Q–V**, Leaf bases, **Q**, cordate; **R**, hastate; **S**, sagittate; **T**, auriculate; **U**, oblique; **V**, truncate. **W–GG**, Leaf tips, **W**, aristate; **X**, caudate; **Y**, acuminate; **Z**, acute; **AA**, cuspidate; **BB**, mucronate; **CC**, apiculate; **DD**, obtuse; **EE**, retuse; **FF**, emarginate; **GG**, obcordate. Drawn by H.Hewson.

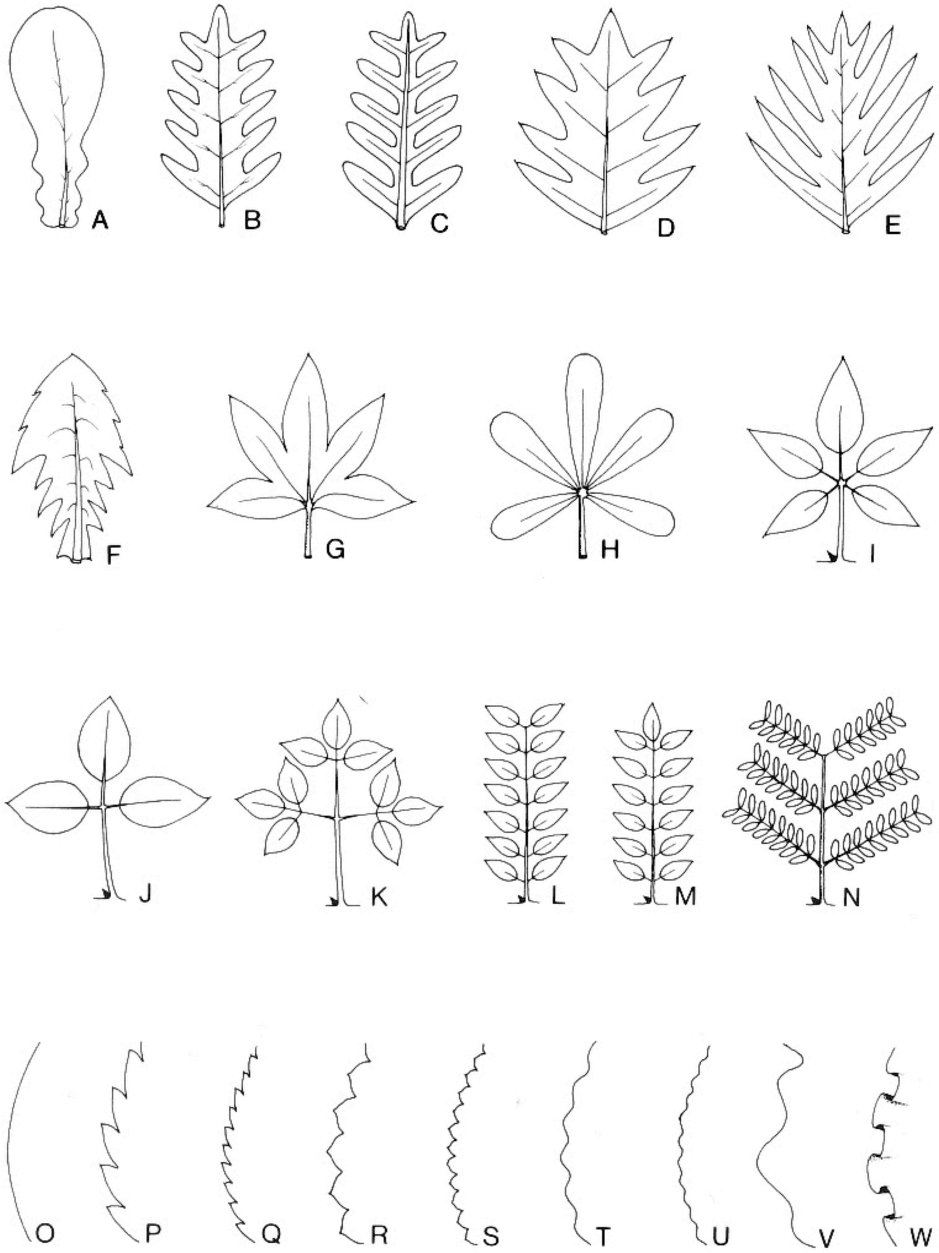

Figure 127. Division of leaves. **A**, lyrate; **B**, pinnatifid; **C**, pinnatisect; **D**, incised; **E**, laciniate; **F**, runcinate; **G**, palmatifid; **H**, palmatisect (=digitate); **I**, palmate; **J**, trifoliolate; **K**, ternate (strictly, biternate); **L–M**, pinnate (**L**, paripinnate; **M**, imparipinnate); **N**, bipinnate; **O**, entire; **P**, serrate; **Q**, serrulate; **R**, dentate; **S**, denticulate; **T**, crenate; **U**, crenulate; **V**, sinuate; **W**, undulate. Drawn by H.Hewson.

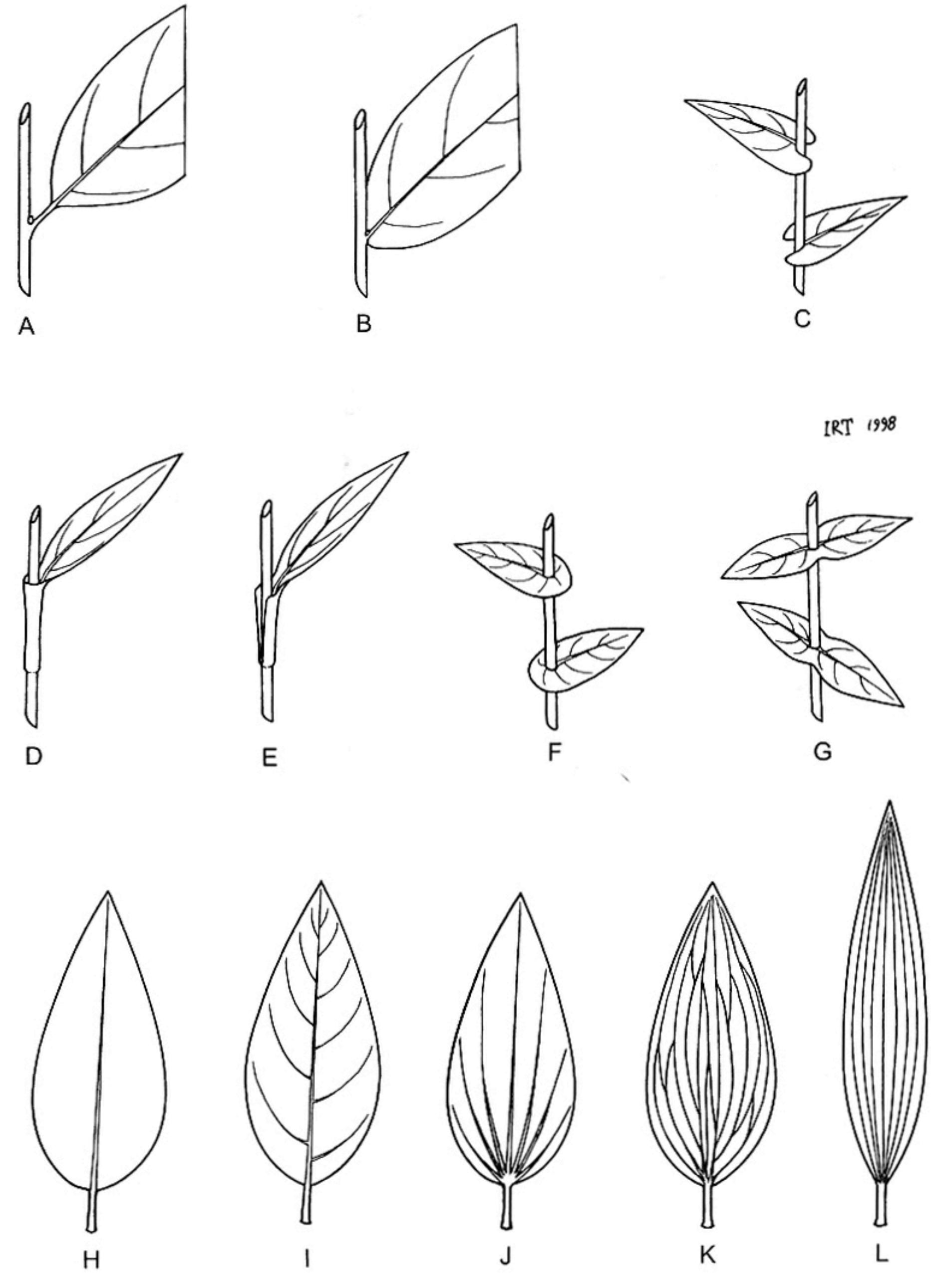

Figure 128. A–G, Leaf attachment. **A**, petiolate; **B**, sessile; **C**, amplexicaule; **D**, closed sheath; **E**, open sheath; **F**, perfoliate; **G**, connate. **H–L**, Leaf venation. **H**, I-veined **I**, pinnate; **J**, palmate; **K**, longitudinal; **L**, parallel. Drawn by I.Telford.

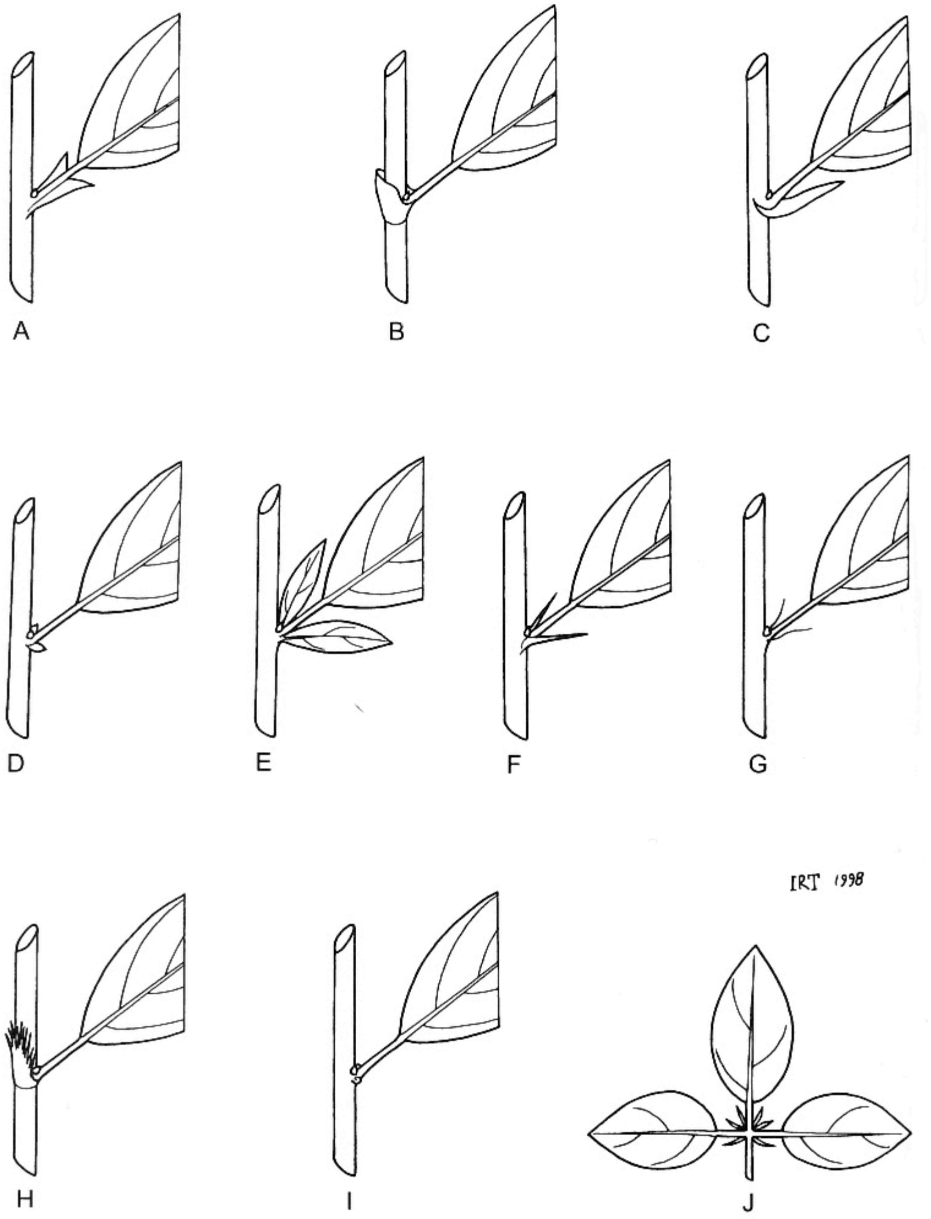

Figure 129. Stipules. **A**, adnate to petiole; **B**, ochreate; **C**, encircling petiole base; **D**, scale-like; **E**, leafy; **F**, spine-like; **G**, hair-like; **H**, lacerate; **I**, gland-like; **J**, stipellae. Drawn by I.Telford.

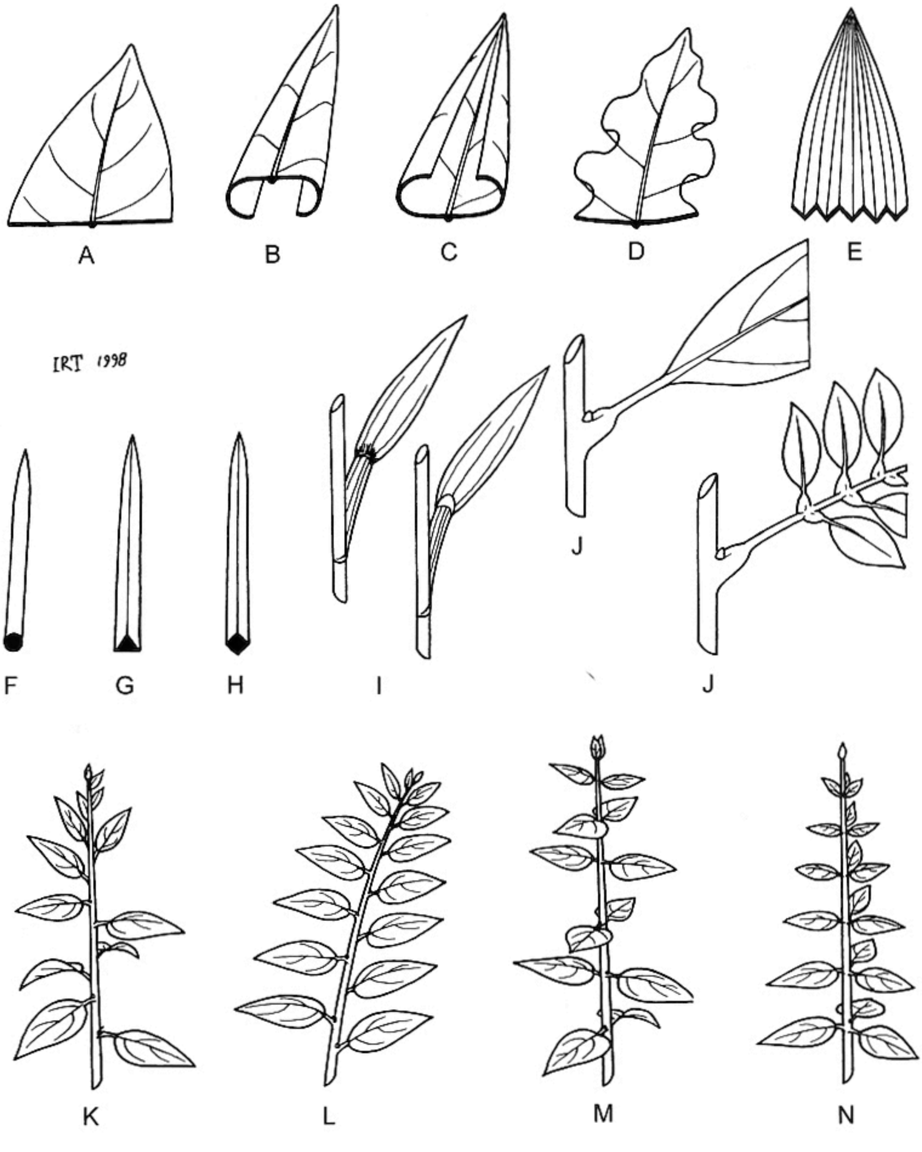

Figure 130. **A–E**, Leaf marginal deflection. **A**, flat; **B**, revolute; **C**, involute; **D**, undulate; **E**, plicate; **F**–**H**, Leaf 3-dimensional shape. **F**, terete; **G**, triangular; **H**, quadrangular; **I**, ligule; **J**, pulvinae. **K–N**, Leaf arrangement. **K**, alternate (spiral); **L**, alternate (distichous); **M**, opposite; **N**, whorled. Drawn by I.Telford.

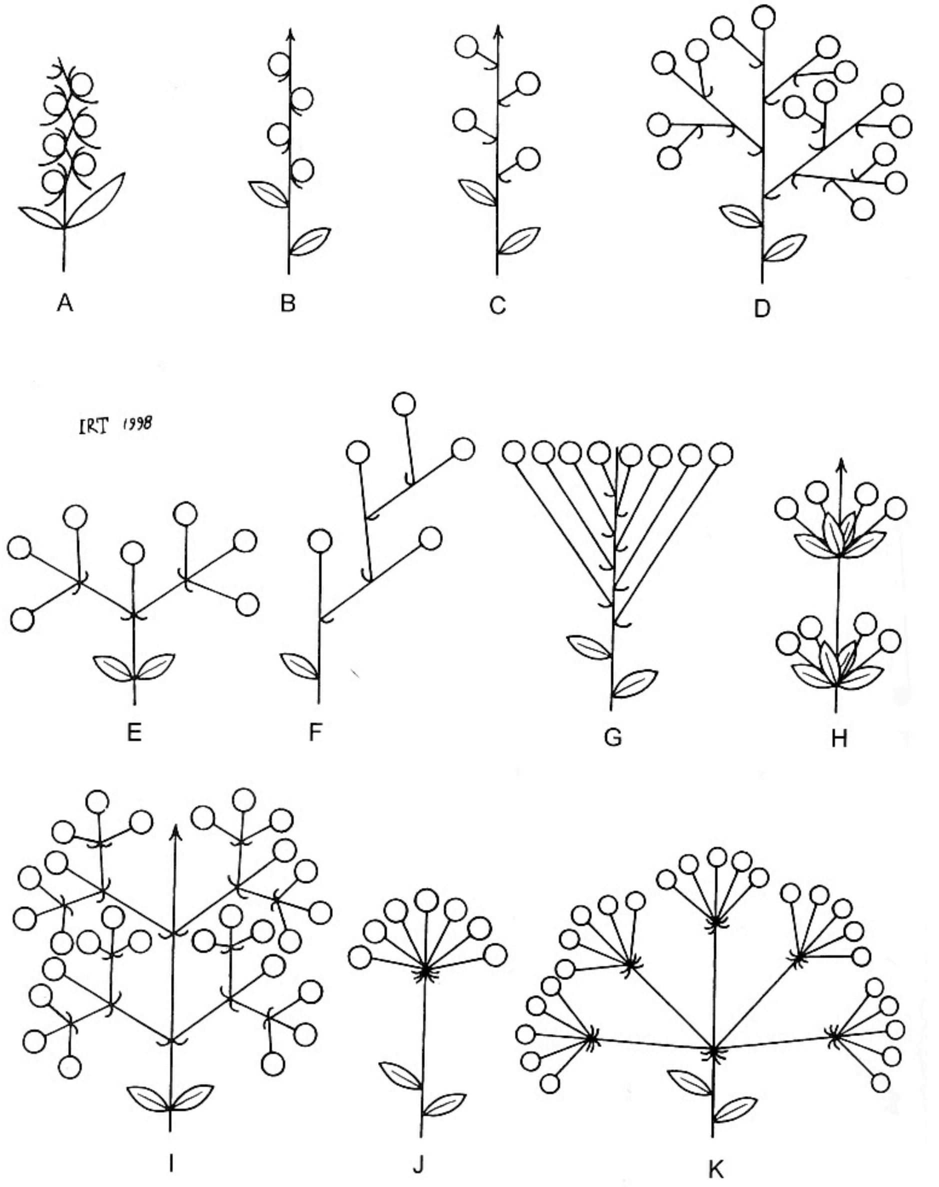

Figure 131. Inflorescence types. **A**, spikelet; **B**, spike; **C**, raceme; **D**, panicle; **E**, dichasial cyme; **F**, monochasial cyme; **G**, corymb; **H**, verticillaster; **I**, thyrse; **J**, umbel; **K**, compound umbel (arrow = vegetative bud; circle = flower). Drawn by I.Telford.

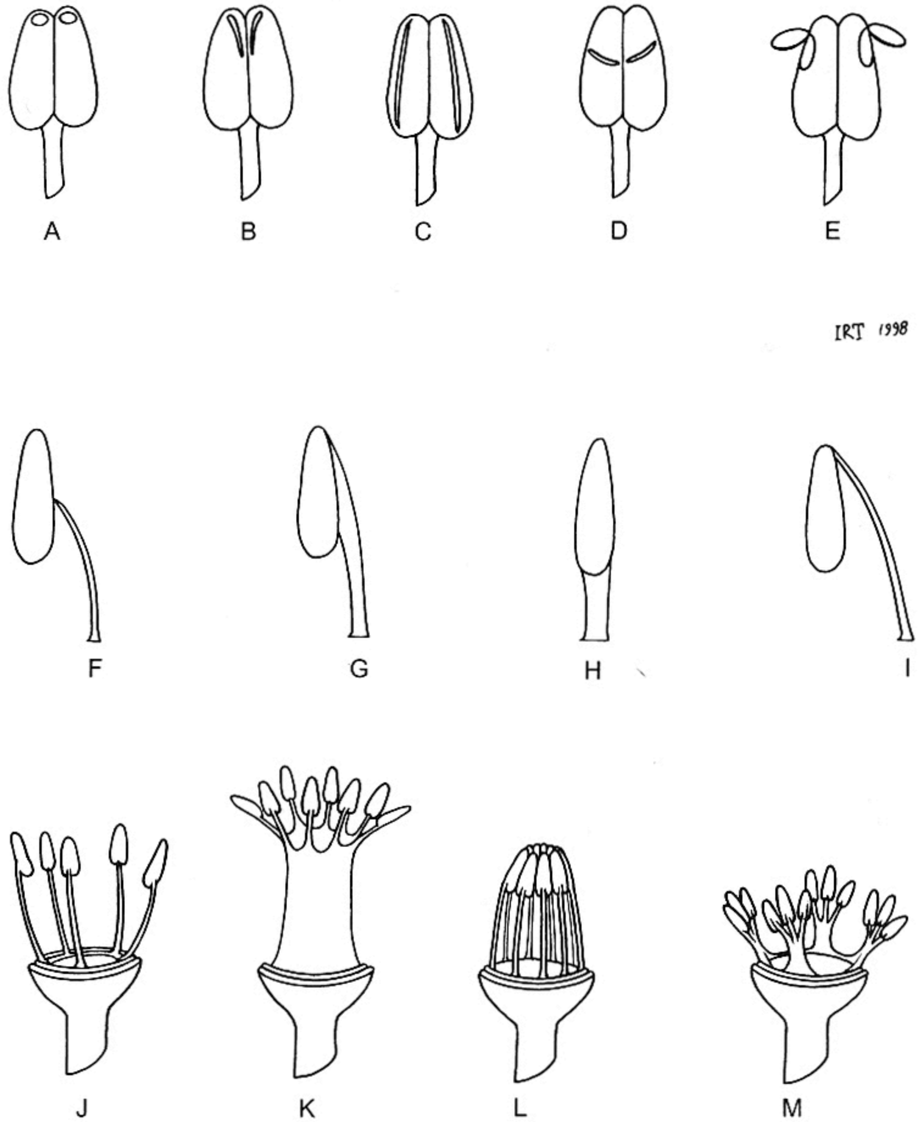

Figure 132. A–E, Anther dehiscence. **A**, pores; **B**, short slits; **C**, longitudinal slits; **D**, transverse slits; **E**, valves; **F–I**, Anther attachment to filament **F**, dorsal versatile; **G**, dorsal not versatile; **H**, basal; **I**, apical. **J–M**, Stamen fusion. **J**, free of each other; **K**, united into a tube; **L**, fused by anthers; **M**, grouped by bundles. Drawn by I.Telford.

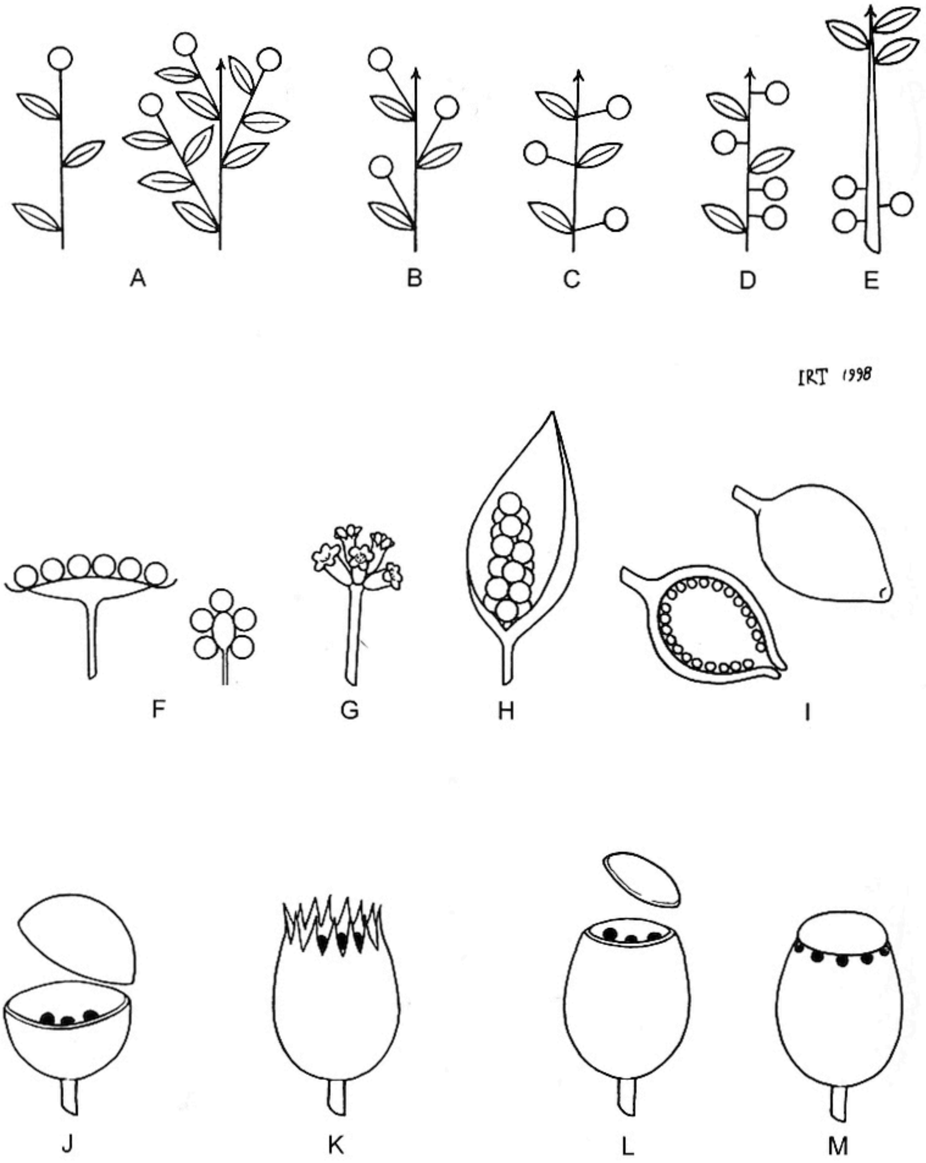

Figure 133. **A–E**, Flower (or inflorescence) position. **A**, terminal; **B**, axillary; **C**, leaf-opposed; **D**, intercalary; **E**, cauliflorous. **F–I**, Unusual inflorescence types. **F**, capitula (heads); **G**, glomerule; **H**, spadix with spathe; **I**, syconiums (figs) (arrow = vegatitive bud; circle = flower or inflorescence). **J–M**, Capsule dehiscence **J**, circumscissile; **K**, denticidal; **L**, operculate; **M**, poricidal. Drawn by I.Telford.

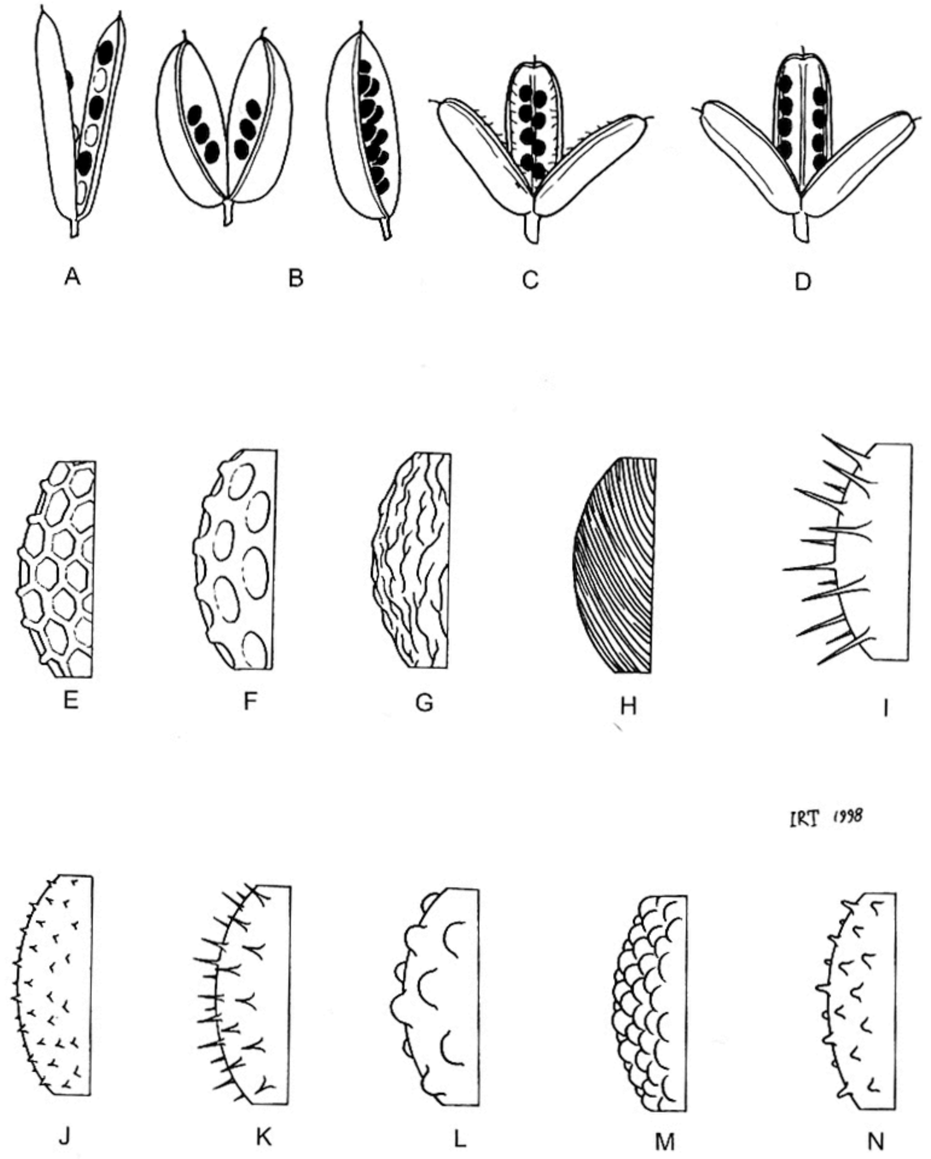

Figure 134. A–D, Fruit showing dihiscence. **A**, pod; **B**, follicle; **C–D**, capsule (**C**, septicidal dehiscence; **D**, loculicidal dehiscence). **E–N**, Seed ornamentation. **E**, reticulate; **F**, foveate; **G**, irregular wrinkles; **H**, striations; **I**, spinulose; **J**, muricate; **K**, echinate; **L**, tuberculate; **M**, colliculate; **N**, papillose. Drawn by I.Telford.

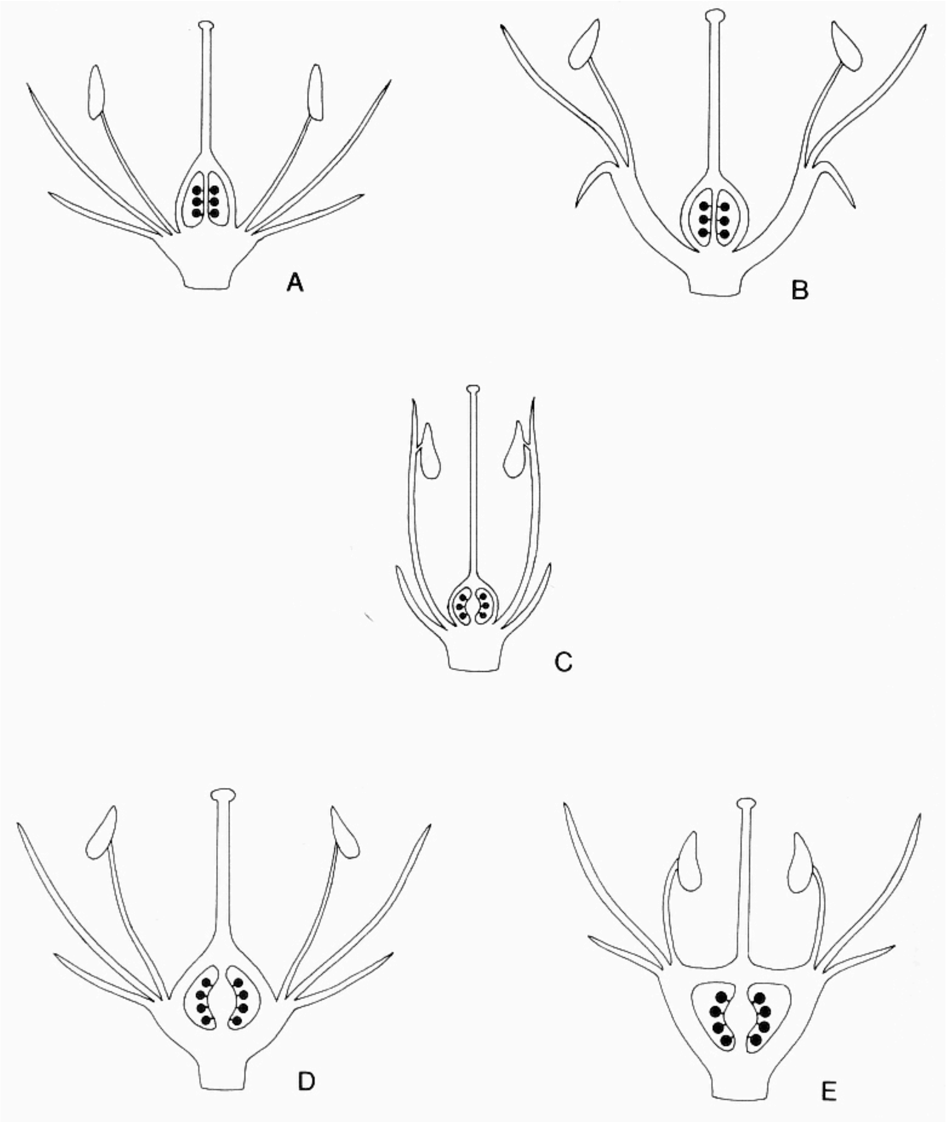

Figure 135. Positions of floral organs. **A**, perianth and stamens hypogynous, ovary superior; **B**, perianth and stamens perigynous, ovary superior; **C**, perianth and stamens hypogynous, stamensepipetalous, ovary superior; **D**, perianth and stamens epigynous, ovary half-inferior; **E**, perianth and stamens epigynous, ovary inferior. Drawn by H.Hewson.

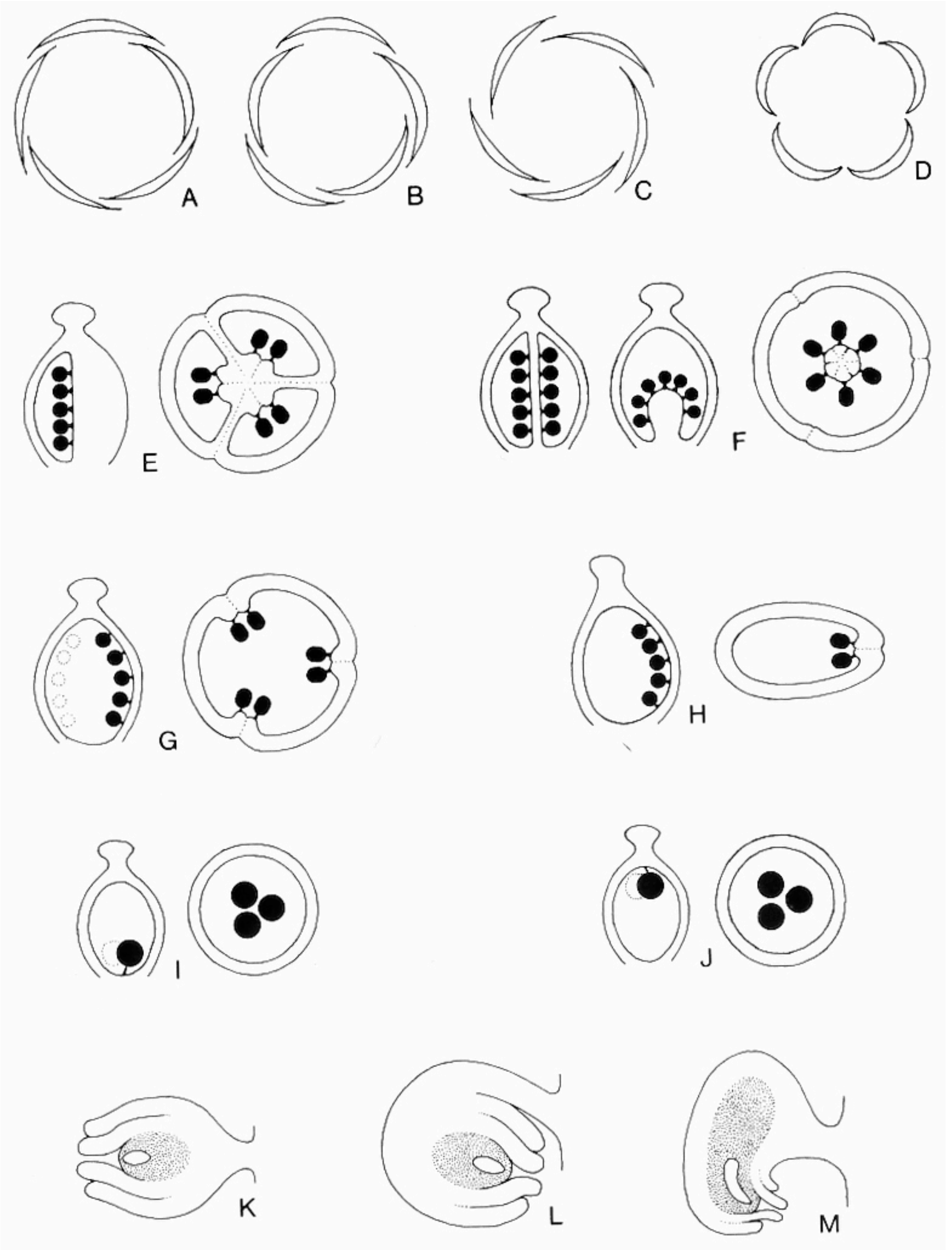

Figure 136. **A–D**, Aestivation. **A–C**, imbricate (**A**, cochlear; **B**, quincuncial; **C**, convolute); **D**, valvate. **E–J**, Placentation. **E**, axile; **F**, free-central; **G**, parietal; **H**, marginal; **I**, basal; **J**, apical. **K–M**, Orientation of ovules. **K**, orthotropous; **L**, anatropous; **M**, campylotropous. Drawn by H.Hewson.

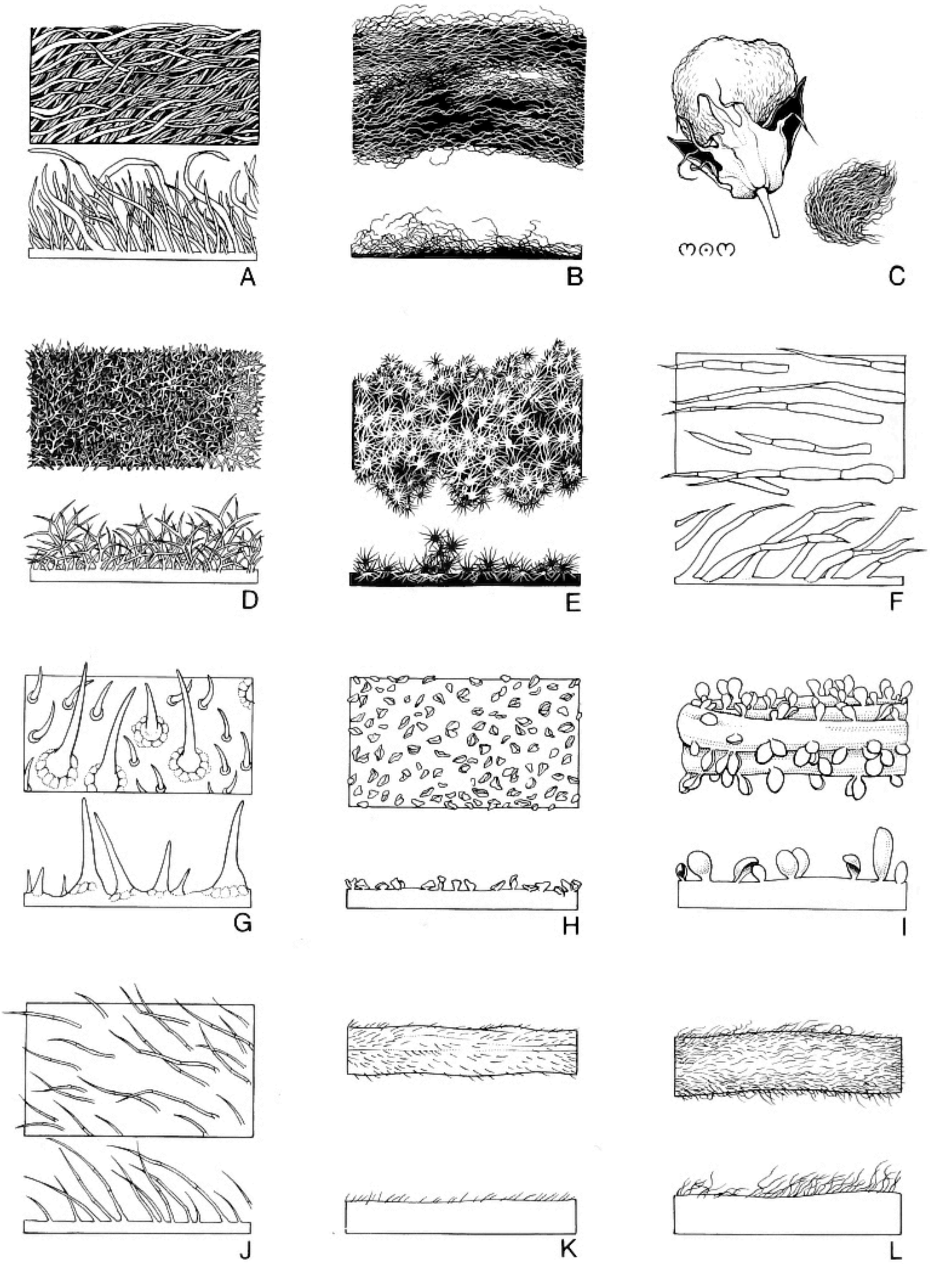

Figure 137. Indumentum types. **A**, chaffy; **B**, cobwebbed; **C**, cottony; **D**, felted. **E**, floccose; **F**, hirsute; **G**, hispid; **H**, mealy; **I**, papillose; **J**, pilose. **K**, puberulous; **L**, pubescent. Drawn by M.Wilson (formerly Menadue).

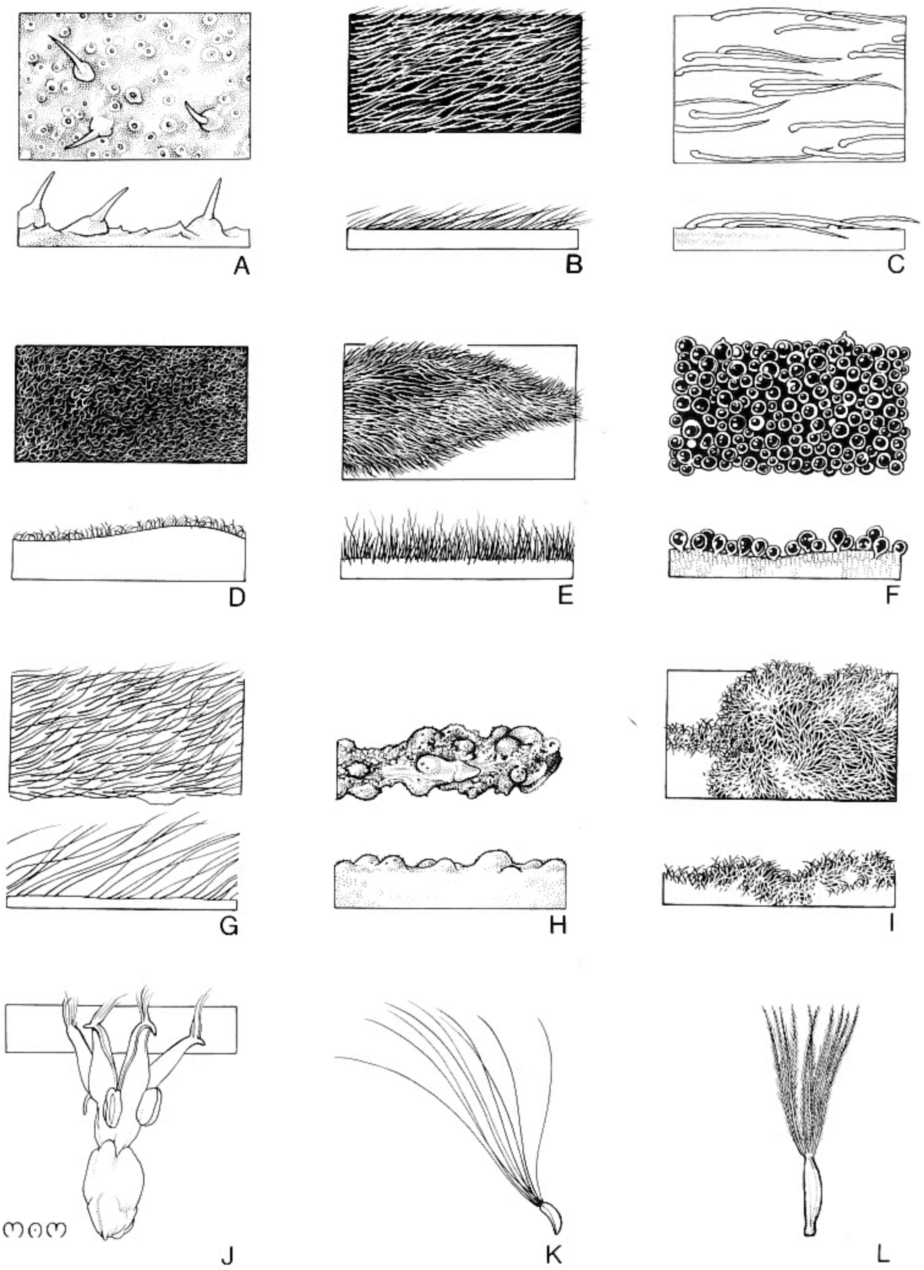

Figure 138. Indumentum types **A**, scabrous; **B**, silky; **C**, strigose; **D**, tomentose. **E**, velvety; **F**, vesciculose; **G**, villous; **H**, warty; **I**, woolly; **J**, bearded. **K**, coma; **L**, pappus. Drawn by M.Wilson (formerly Menadue).

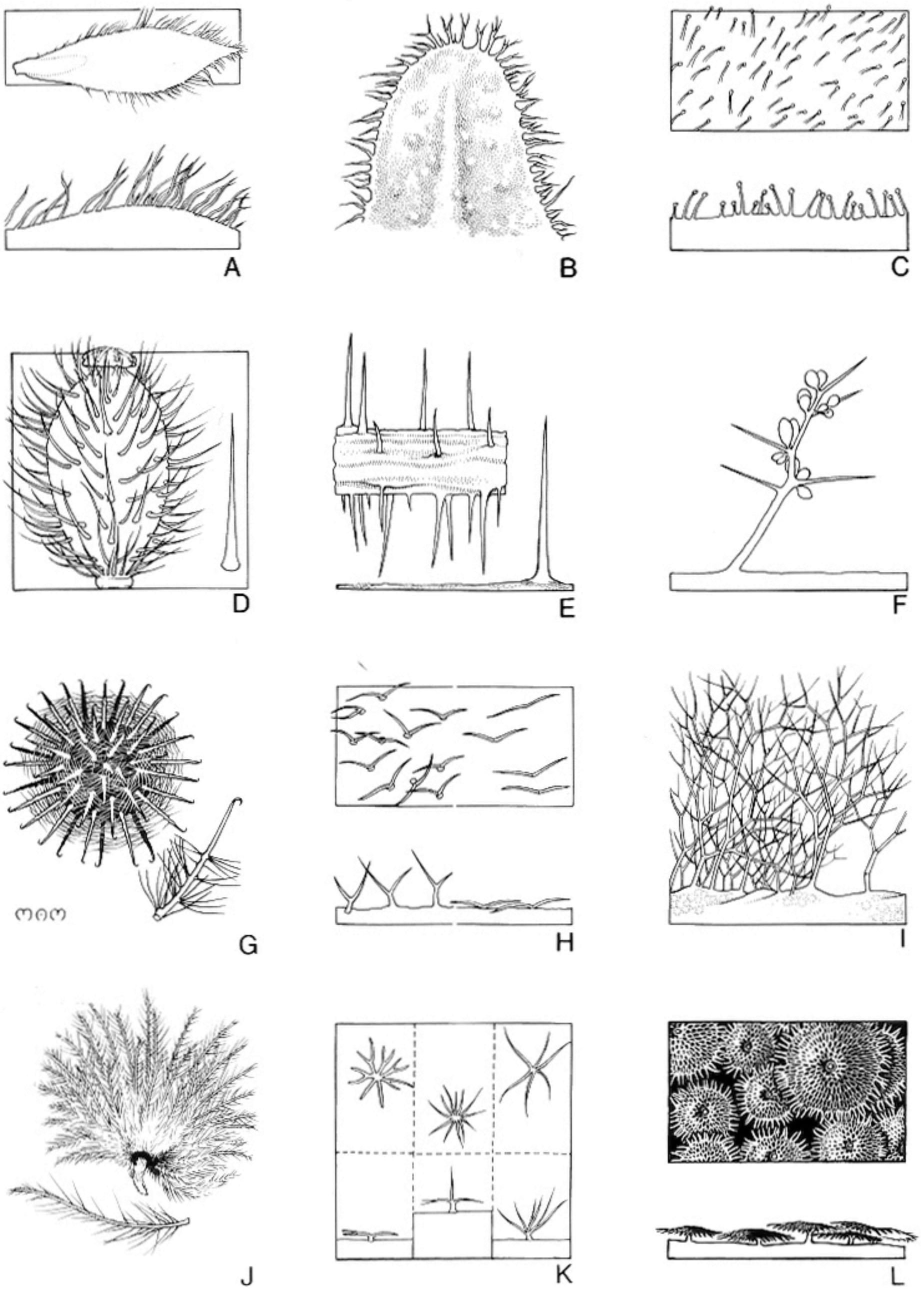

Figure 139. Trichome types **A**, ciliate; **B**, fimbriate; **C**, mucilage trichome; **D**, bristle. **E**, prickle; **F**, spine; **G**, barbed trichome; **H**, bifid trichomes; **I**, dendritic trichomes; **J**, plumose trichomes; **K**, stellate trichomes; **L**, peltate scales. Drawn by M.Wilson (formerly Menadue).

Abbreviations and Contractions

Literature

Author abbreviations follow R.K.Brummitt & C.E.Powell, *Authors of Plant Names* (Royal Botanic Gardens, Kew, 1992).

Journal titles are abbreviated in accordance with G.H.M.Lawrence *et al.*, *Botanico-Periodicum-Huntianum* (Hunt Botanical Library, Pittsburgh, 1968) and G.D.R.Bridson & E.R.Smith, *Botanico-Periodicum-Huntianum/Supplementum* (Hunt Institute for Botanical Documentation, Pittsburgh, 1991).

Other literature is abbreviated in accordance with F.A.Stafleu & R.S.Cowan, *Taxonomic Literature*, 2nd edn (Bohn, Scheltema & Holkema, Utrecht, 1976–1987), except that upper case initial letters are used for proper names and significant words. The *Flora of Australia* is abbreviated to *Fl. Australia*.

Herbaria

Abbreviations of herbaria are in accordance with P.K.Holmgren, N.H.Holmgren & L.C.Barnett, *Index Herbariorum* Part I, 8th edn (New York Botanical Garden, 1990). Those most commonly cited in the *Flora* are:

AD	State Herbarium of South Australia, Adelaide
BM	The Natural History Museum, London
BRI	Queensland Herbarium, Brisbane
CANB	Australian National Herbarium, Canberra
CBG	Australian National Botanic Gardens Herbarium, Canberra
DNA	Northern Territory Herbarium, Darwin
HO	Tasmanian Herbarium, Hobart
K	Royal Botanic Gardens, Kew
MEL	National Herbarium of Victoria, Melbourne
NSW	National Herbarium of New South Wales, Sydney
PERTH	Western Australian Herbarium, Perth
QRS	Australian National Herbarium, Atherton

States, Territories

Abbreviations of Australian States and Territories as used in statements of distribution and citation of collections are:

A.C.T.	Australian Capital Territory
N.S.W.	New South Wales
N.T.	Northern Territory
Qld	Queensland
S.A.	South Australia
Tas.	Tasmania
Vic.	Victoria
W.A.	Western Australia

Abbreviations and contractions

General abbreviations

add.	addendum
agg.	aggregate species
alt.	altitude
app.	appendix
auct.	*auctoris/auctorum* (of an author or authors)
auct. mult.	*auctorum multorum* (of many authors)
auct. non	*auctorum non* (of authors [but] not....), used for misapplied names
c.	*circa* (about)
cf.	*confer* (compare)
Ck	Creek
cm	centimetre
coll.	collector
colln	collection
comb.	*combinatio* (combination)
cons.	*conservandus*
cult.	cultivated
cv.	cultivar
d.b.h.	diameter at breast height
Dept	Department
descr.	*descriptio*
diam.	diameter
E	east
ed./eds	editor/editors
edn	edition
e.g.	*exempli gratia* (for example)
et al.	*et alii*/*et aliorum*; and others/and of others
f.	*forma* (form)
fam.	*familia* (family)
fig./figs	figure/figures (in other works)
Fig.	Figure/Figures (in this volume of the *Flora*)
gen.	*genus* (genus)
gen. nov.	*genus novus* (new genus)
Gt	Great
holo	holotype
hort.	*hortus* (garden) or *hortensis* (of a garden)
HS	Homestead
Hwy	Highway
i.e.	*id est* (that is)
ined.	*ineditus* (unpublished)
in litt.	*in litteris* (in correspondence)
in obs.	*in observatio* (in observation)
Is.	Island/s
iso	isotype
isolecto	isolectotype
km	kilometre
kt	kilotonne
L.	Lake
L.A.	Logging Area
lat.	latitude
lecto	lectotype
loc. cit.	*loco citato* (in bibliographic citations: in the same work and page as just cited)
loc. id.	*loco idem* (in specimen citations: in the same place as just cited)

long.	longitude
L.S.	longitudinal section
l:w	length to width ratio
m	metre
mm	millimetre
Ma	million years ago
Mt/Mts	Mount/Mounts
Mtn/Mtns	Mountain/Mountains
N	north
n	haploid chromosome number
2n	diploid chromosome number
Natl	National
n.d.	no date
NE	north-east (ern)
nom. cons.	*nomen conservandum* (conserved name)
nom. cons. prop.	*nomen conservandum propositus* (proposed conserved name)
nom. illeg.	*nomen illegitimum* (illegitimate name)
nom. inval.	*nomen invalidum* (name not validly published)
nom. nov.	*nomina nova* (new name)
nom. nud.	*nomen nudum* (name published without a description or reference to a published description)
nom. prov.	*nomen provisorium* (provisional name)
nom. rej.	*nomen rejiciendum* (rejected name)
nom. superfl.	*nomen superfluum* (superfluous name)
nov.	*novus/*new
n. ser.	new series
n.v.	*non vidi* (not seen)
NW	north-west (ern)
op. cit.	*opere citato* (in the work cited above)
opp.	opposite
orth.	orthography, orthographic
p./pp.	page/pages
penin.	peninsula
pers. comm.	by personal communication
pl./pls	plate/plates
prep.	preparation
p.p.	*pro parte* (in part)
p.p. max	*pro parte maxima* (the larger part)
p.p. min	*pro parte minore* (the smaller part)
q.v.	*quod vide* (which see)
R.	River
Ra.	Range
Rd	Road
rly	railway
S	south
SE	south-east (ern)
sect.	*sectio* (section)
SEM	Scanning Electron Micrograph
ser.	series
S.F.R.	State Forest Reserve
s. lat.	*sensu lato* (in a wide sense)
s. loc.	*sine loco* (without locality)
s.n.	*sine numero* (without number)
sp./spp.	species (singular/plural)

sp. aff.	*species affinis* (species related to)
sp. nov.	*species nova* (new species)
s. str.	*sensu stricto* (in a narrow sense)
St	Street
stat.	*status* (status)
Stn	(pastoral) Station
subg.	subgenus
subsp./subspp.	subspecies (singular/plural)
subsp. nov.	*subspecies nova* (new subspecies)
suppl.	supplement
SW	south-west (ern)
syn	syntype
synon.	synonym
T	Type (collection)
t./tt.	*tabula/tabulae* (plate/plates)
T.R.	Timber Reserve
trib.	*tribus* (tribe)
trig.	trigonometric station
T.S.	transverse section
typ. cons.	*typus conservandus* (conserved type)
var.	*varietas/*variety
viz.	*videlicet* (namely)
vs	versus
UV	ultraviolet
W	west
x	basic chromosome number

Symbols

†	taxon included in key but not treated further in text
*	naturalised taxon, not originally native
#	native taxon now naturalised in Australia beyond its natural range
[ ]	misapplied name or *nomen invalidum*; also, in localities, denotes a place name later than that originally cited or on the herbarium sheet
±	*in species descriptions*, more or less
±	*in lichen chemistry*, with or without
<	less than
≤	less than or equal to
>	more than
≥	more than or equal to
µm	micrometre
♀	female
♂	male

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Scientific names at and below genus, names of Conventions, Acts and other legislation, book titles and ship names are in *italic.*

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ISBN 0643059652
9 780643 059658

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